1921

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

LIBERATION OF ORGANIC MATTER BY ROOTS OF GROWING PLANTS

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ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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T. L. LYON AND J. K. WILSON

In the course of an investigation under way at this station, it became desirable to know whether organic matter, particularly that of a nitrogenous nature, is liberated by the roots of growing plants, at least of the plants commonly raised on farms in this region. Numerous investigations conducted elsewhere have shown that nitrogen is lost by certain plants during the late stages of growth, particularly about the ripening period. There seemed to be a question, however, whether this nitrogen escaped from the leaves or the roots, and it had never been shown to be in the form of organic matter. The previous investigations had, indeed, not touched on the question of the loss of organic matter by growing plants, and aside from its bearing on the investigation in hand this appeared to be a matter of some scientific interest.

A closely related question is the possible liberation of reducing or oxidizing substances by the roots of growing plants. There had previously been some investigation of this subject, but since the experiments on the liberation of organic matter furnished exceptionally good opportunities for making the tests for catalysts it was decided to try to obtain some information to supplement the previous work.

REVIEW OF LITERATURE CONCERNING LOSS OF NITROGEN FROM GROWING PLANTS

A large amount of work has been reported showing the percentage of the various nutritive elements found in crops at certain stages of growth. Less work has been done, however, on the actual weight of nutrients in plants during their growth and maturity.

The work of Wilfarth, Römer, and Wimmer (1906) was concerned with the assimilation of the elements of nutrition by plants during different periods of their growth. This investigation extended over a period of about eight years. The experiments included both field and pot work, the former with barley, spring wheat, and potatoes, and the latter with

barley, peas, potatoes, and mustard. The plants were harvested at different stages of growth. These plants were carefully divided into their component parts — roots, stems, ears, and so on — and were dried, weighed, and analyzed. The results as stated below are based on pounds of nitrogen in the crop.

The barley was planted on March 30 and the cuttings were made on May 29, June 17, July 3, and July 27. The plant parts were separated and grouped into aboveground parts and underground parts. Separate analyses were made of stems, green leaves, yellow leaves, ear stalks, awns, straw, grain, roots, and stubble. Total weights of nitrogen showed that this nutrient was present in its greatest amount on June 17 (presumably when the plants were in bloom) and that the mature cutting of July 27 had lost 25 per cent of the total nitrogen.

The wheat was planted on April 23 and was harvested on June 22, July 14, August 5, and August 28. The methods used were the same as for barley. In the case of the wheat, the nitrogen was found in its greatest amount in the third cutting, on August 5, and the mature crop showed a loss of about 20 per cent of the total nitrogen.

The potatoes were planted on April 28 and analyses were made of the various parts of the plant. Four different harvests were gathered as the crop was maturing. The results were quite different from those with barley or with wheat. In this case the greatest amount of nitrogen was found in the last harvest, which represents the crop gathered in October.

The barley was planted on April 20 in sand in pots, and was watered with nutrient solutions. Quadruplicate cultures were grown in the greenhouse. On May 11 stems had commenced to show. The first harvest was made on May 24, the second on June 1, the third on June 12, the fourth on June 25, the fifth on July 20. The harvest consisted of both roots and tops. In one series the greatest weight of nitrogen was found on June 25, in the other three on June 12. From these dates on to maturity there was a loss of total nitrogen ranging from 9 to 26 per cent.

The peas were planted and tended in a similar manner to the barley, with the same dates for planting and harvesting. The weight of nitrogen in the harvested crops was greatest on June 25 in three cases, and in the fourth case at the last harvest. The decrease toward maturity in the three cases ranged from 9 to 30 per cent.

The potatoes were grown in turf and sand in the greenhouse. Applications of fertilizer were made so that plant nutrients would not be deficient. Harvests were made on June 12, June 30, August 7, and September 14. The plant parts were divided into foliage and tubers. The figures for weight of nitrogen show that there was a constant decrease of this constituent in the foliage after the first harvest, altho there was a constant increase in the weight of the tubers. The total plant, however, had its greatest amount of nitrogen on August 7, with a decrease of 6.46 per cent thirty-eight days later.

Pots containing 5.3 kilograms of dry earth received fertilizers to stimulate growth of plants and to furnish an abundant supply of nutrients. The seeding of mustard was done on May 7, and subsequently all pots contained six plants. The experiment was run in duplicate. The mustard was harvested, first, on the appearance of the first pods, second, when the formation of seed was complete, and third, at maturity. Analysis of the total plant only was made. The total nitrogen was greatest when the formation of seed was complete. The loss at the third harvest was about 10 per cent of the total nitrogen.

With the intention of verifying the results obtained by Wilfarth, Römer, and Wimmer, André (1912) cut barley at five different stages of growth from equal areas of land and analyzed the dry harvest. The cuttings were made (1) when the heads began to show, (2) when the barley was in bloom, (3) when seed began to form, (4) at the mature stage, and (5) beyond the ripe stage. The figures for total nitrogen show 7.023 grams at the first stage, 8.693 at blooming, 10.422 when the fruit was forming, 12.389 at maturity, and 10.360 at the last harvest.

The object of an experiment by Ramsay and Robertson (1918) was to determine the relative proportions of each of the principal nutrient elements contained in the plant at various stages of growth. They grew potatoes in soil in boxes containing about 130 pounds of well-drained and fertilized soil. Approximately the same weight of seed was put in each box. The first harvest was gathered on January 29, thirty-three days after brairding, the second on February 25, the third on March 26, and the last on April 30. At the first three harvests complete recovery of tops and roots was made. The last harvest was more difficult and about 30 per cent of the roots were lost. Cropping, harvesting, and analyzing were done in duplicate in each case. The total nitrogen contained in a 20-ton crop of

potato plants at various stages of development was 69 pounds at the first harvest (thirty-three days), 241.3 pounds at the second harvest (fifty-eight days), 306.7 pounds at the third harvest (eighty-nine days), and 319 pounds at the fourth harvest (one hundred and twenty-four days). There was a constant assimilation of this important element.

Hay was cut by Crowther and Ruston (1911–12) from uniform areas of a crop of grass which had been seeded the previous spring. The grass seed consisted of a mixture of perennial rye grass, Italian rye grass, white clover, trefoil, alsike, English single-cut cow grass, Chilean red clover, and rib grass. The first cutting was made when the rye grass was in full flower. A good growth of leguminous plants showed underneath. The second cutting was made when the rye grass was forming seed and the clovers were beginning to flower. At the third cutting the grasses were ripening and the clovers were in full bloom, while the fourth and last cutting was made when the crop was decidedly ripe. Analysis of the crops showed the greatest total weight of nitrogen to be present at the third cutting, or when the grasses were ripening and the clovers were in full bloom. In the last cutting there was a loss of 25 pounds of nitrogen to the acre.

The work was repeated the following year, but with barley as the crop. The seed was drilled on May 12. Cuttings were made on June 9, June 23, July 7, and July 21, but the stages of growth reached on these dates were not noted. The changes with advancing age as to nitrogen were similar to those observed in the preceding year with grasses.

The changes in chemical composition of the timothy plant during growth and ripening, with comparative studies of the wheat plant, are recorded by Trowbridge, Haigh, and Moulton (1915). Timothy plants, cut from uniform areas, represented the following stages of growth: (1) about one foot high in rapid growth; (2) no heads showing; (3) no stalks in bloom but beginning to head; (4) in full bloom; (5) just out of bloom and seed formed; (6) seed in dough; (7) seed fully ripe; (8) growth the following spring not yet started but leaves green. The plant parts of the samples thus collected were divided into heads, stalks and leaves, hay, and stubble and bulbs. The amounts of the various nutrients determined were recorded in total pounds to the acre. Data from these plants were collected for one year only. The figures for weight of nitrogen showed that there was a gradual increase in this constituent in heads from

all plots. In the stalks and leaves, the nitrogen was found in greatest amounts in two cases when the plants were just out of bloom and the seed was formed, and in the third case when no stalks were in bloom but the plants were beginning to head. In the hay the greatest weight of nitrogen was found when the seed was all in dough. In the stubble and bulbs the greatest amount of nitrogen was present when the seed was fully ripe.

The comparative studies with wheat represent two areas from the same field. The stages of development were: (1) plants green and in bloom; (2) seed formed and in milk; (3) seed in dough; (4) seed fully ripe. The plant parts of the samples were divided into heads, stalks and leaves, plants above ground, and roots and stubble. The figures for nitrogen found in the heads showed a steady increase in this nutrient thruout all the stages. With stalks and leaves there was a constant loss of nitrogen after the first stage as the plant approached maturity. In the plants above ground there was an increase of nitrogen to the seed-in-dough stage and a considerable loss in the fully-ripe stage. Roots and stubble contained their greatest weight of nitrogen at the seed-in-milk stage. If the total plant is considered, the nitrogen reached its greatest amount when the seed was in the dough stage.

The influence of advancing maturity on the composition of timothy was reported by Waters (1915). Results were obtained for five years of investigation, but the results are complete for only three of these years. Uniform areas were harvested at five different stages of growth: (1) when the plants were in full head; (2) when the plants were in bloom; (3) when the seed had formed; (4) when the seed was in dough; (5) when the seed was ripe but not shattered. The greatest weight of nitrogen was found in three of the trials when the plants were in full bloom, and in the other two trials when the seed had formed. The fluctuation in loss of nitrogen between the stages when it was at the maximum and when it was fully ripe ranged from 12 to 38 per cent.

Schulze (1904) cut 100 plants of rye and collected the roots for examination. The cuttings were made forty days after drilling, which was on September 20. On April 22 a second cutting was made. The plants at this stage were very green. On May 20 a third cutting was made. The plants now were in the boot stage. The fourth cutting was made on June 16 and the plants were just thru blooming. The weight of nitrogen

in these stages was as follows: first cutting, 0.153 gram; second cutting, 1.225 grams; third cutting, 2.723 grams; fourth cutting, 2.713 grams.

With wheat only three harvests were made: the first was thirty-seven days after drilling, which took place on September 23; the second was on April 22, and no heads were showing at this date; the third was on June 16, when the plants were thru blooming. The nitrogen in 100 plants was as follows: first period, 0.132 gram; second period, 0.596 gram; third period, 1.802 grams. No later analyses are given, and thus it is not clear whether there was a loss in weight of nitrogen after the blooming period.

Le Clerc and Breazeale (1909) state that the loss of nutrients from plants may be explained in one of three ways: (1) by the backward flow of the salts of the plant juices thru the stems and roots to the soil; (2) by the decay or dying and falling off of leaves; or (3) by the action of rain, dew, wind, and other climatic agencies. Or there may be a combination of all these causes to a limited extent. In support of the third possibility, these investigators conducted experiments designed to imitate these climatic agencies. Barley plants were grown in soil contained in Wagner pots, and no water was allowed to come in touch with the aboveground parts during the growing period. Just at the heading period the whole plant was harvested, placed in a large evaporating dish, and soaked with water for several minutes. After drying, this operation was repeated. The plants were then dried and analyzed. The results show that 1.6 per cent of the entire content of nitrogen was lost on washing.

Wheat plants were harvested at three periods of growth — bloom, early ripeness, and full ripeness. The plant parts were divided into stems and straw, and heads. They were separately washed or soaked for from five to ten minutes. The wash water was analyzed, as were also the dried stems and straw and the heads. The results show that at bloom 1.4 per cent of the nitrogen was washed out, while at full maturity 7 per cent was found in the wash water.

Results were obtained also from apple twigs. Two twigs containing green leaves were gathered and washed for a few minutes with distilled water. They were then set aside, with their butt ends immersed in water, until the leaves were unquestionably dead, when they were again washed and analyses were made of both washings and residues. The results of the analyses showed that thru the action of water about 3 per cent of nitrogen had been washed out.

Two pots of wheat were kept in the greenhouse until the wheat was completely ripe. They were then placed out of doors, where they were subjected to four rainfalls on separate days. The pots were so arranged that the washings were caught in a tray. These washings, equivalent to about one inch of rainfall, dissolved from the plant 27 per cent of the nitrogen as well as other nutrients.

Two oat pots were placed out of doors as were the wheat pots. The plants were about eight inches high. They were allowed to grow in this position until they were ripe. They were exposed to three rains during this time. The leachings contained 2 per cent of the nitrogen, as well as other nutrients.

In two pots of potatoes, the aboveground parts were washed with 2.5 quarts of water in a very fine spray. This was done when the plants were twenty-four inches high, when they were beginning to ripen, and when they were completely ripe. The leachings and the plant parts above ground were analyzed. The results show that, due to the action of washing, 7.5 per cent of the nitrogen was washed out.

Jones and Huston (1914) report the composition of the maize crop at stages corresponding in the main with those at which the crop would be used for practical purposes, such as soiling, ensiling, and grain production. Conditions of uniformity were maintained as nearly ideal as it was possible to have them. In order to insure adequate moisture, the field was irrigated when necessary so as to provide not less than one inch of water every week. The soil was in a good state of fertility. Analyses were made as follows: (1) when the plants had six leaves, June 16; (2) when the plants were about four feet high, July 24; (3) when tassels began to form, August 6; (4) when the maize was fully pollinized, August 28; (5) when the plants were in the medium milk stage, with the pollen all shed and the silks brown, September 10; (6) when the kernels were glazing, September 24; (7) when the kernels were hardening, this being the ensiling stage, October 1; (8) when the maize was ready to put into shock, October 8; (9) when the maize was fully cured and ready to be stored, November 12.

The samples represented the crop cut at the soil level. Data for weight of nitrogen showed a gradual increase from the first analysis to October 8, the amount at first being 0.28 pounds an acre and increasing to 110.6 pounds on the last-named date. At the last analysis, on November 12,

which represented samples left in the field and in the shock, for the former a loss of about 23 pounds was shown, while for the latter a slight gain was reported. This loss of nitrogen when the plants were left in the field after October 8 was from both ears and stalks. In the former there was a loss of 9.2 pounds in the field and a gain of 7.6 pounds in the shock; in the latter there was a loss of 15 pounds in the field and a loss of only 2.1 pounds in the shock.

Taking the results of these investigations as a whole, there appears to be in nearly all cases a loss of nitrogen from grass and small grains at some time between the period of full bloom and complete maturity. In maize this occurs if the plants are allowed to ripen when connected with the roots, but potatoes showed no loss of nitrogen in the Bernburg and Australia experiments, and only a small loss in those of Le Clerc and Breazeale.

OBJECT OF THE PRESENT EXPERIMENTS

The experiments herein described had two more or less distinct objects. The first was to ascertain whether growing plants liberate organic matter and, if they do, to determine at what stage of growth this takes place and what relation it bears to the absorption of nitrate nitrogen by the plant. The second object was to detect, if possible, the presence of reducing and oxidizing ferments in the nutrient solutions in which the plants used for the first investigation were grown.

METHODS USED

The plants used in these experiments were grown in water culture. This was done in order that an intimate study might be made of the plant as it grew and the solution as it was being drawn upon by the plant for various nutrients, especially nitrogen. Since a number of organic bodies may be given off by the developing plant, these may not be present when the nutrient solution is analyzed if it is allowed to become infected with molds or bacteria. Therefore, in order that this solution should represent the action of the plant alone, a method for growing the root system in contact with the nutrient solution without infection was used. This method has been published, together with data showing its reliability (Wilson, 1920). A description of the method follows.

SEED STERILIZATION

Seeds were rendered sterile by the calcium hypochlorite method as employed by Wilson (1915). After disinfection the seeds were planted on a sterile medium, from which, after germination, the plants were transferred to the permanent position. The solid medium for the germination was usually composed of the same ingredients as were used in the large containers, from which the plants eventually drew their nutrients, with from 1 to 1.5 per cent of agar. The agar was used in order that contaminations might be detected before the plants were transferred to their permanent position. This medium was made in sufficient quantity to meet the requirements and was distributed into large test tubes.

Since the roots of most plantlets spread out in a lateral direction, thus making it difficult to transplant them quickly and conveniently, some device was needed which would direct the root growth in a vertical direction. To accomplish this there was placed in each test tube a short piece of glass tubing, 25 by 50 millimeters in size (fig. 1, *e*). A sufficient quantity of the medium was put into the tube to cover all but about 15 millimeters of this glass tubing. After sterilization of the medium the sterile seeds were dropped onto it, where they germinated and produced rootlets for subsequent use. When the roots

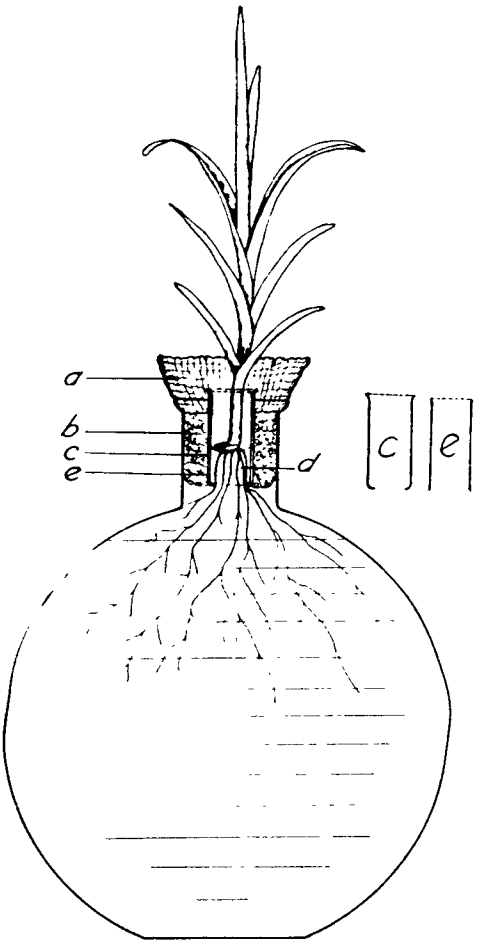

FIG. 1. DEVICE FOR GROWING LARGE PLANTS IN STERILE MEDIA

a, Cheesecloth; *b*, cotton wool; *c*, outside tube into which *e* slides; *d*, agar carried over from test tube with plantlet; *e*, tube in which seed germinates

FIG. 2 OAT PLANT GROWN IN STERILE SOLUTION FOR 105 DAYS

(Table 1, serial no 1272)

present in the form of HNO_3. (The quantity of soluble organic matter in the plant solutions was not great enough to interfere with the proper nitration of the phenoldisulfonic acid.)

Ammonia was determined by direct nesslerization.

Organic nitrogen in the plant solutions was determined according to the method described by the American Public Health Association (1905).

The total organic matter in the solutions was determined by evaporating 100 cubic centimeters of the filtered solution and igniting the residue thus obtained at dull red heat. The loss on ignition was reported as organic matter.

The dry weight of the deposit in the bottom of each flask was ascertained by transferring it to a filter, drying it at 110° C., and weighing it, the weight of the dry filter being subtracted from the total weight.

The amount of organic nitrogen in the deposit in the bottom of each flask was found by transferring the filter and contents from the previous determination to a Kjeldahl flask, digesting by the Gunning method, neutralizing the excess acid with ammonia-free Na_2CO_3, and distilling off the ammonia, which was nesslerized.

TESTS FOR THE PRESENCE OF ORGANIC NITROGEN IN NUTRIENT SOLUTIONS IN WHICH PLANTS OF SEVERAL KINDS HAD GROWN

Several different kinds of seeds were germinated under aseptic conditions, and were transplanted, in the manner described, to flasks containing the usual nutrient solution of one-tenth strength. The manner of growth of the plants in these flasks is shown in figures 2 to 4.

FIG. 3. MAIZE PLANTS GROWN IN STERILE SOLUTION FOR 189 DAYS

(Table 1, serial no. 1303)

FIG. 4. PEA PLANT GROWN IN STERILE SOLUTION FOR 139 DAYS

(Table 1, serial no 1280)

In one flask the usual nutrient solution was not employed, as it was desired to ascertain whether a leguminous plant grown in a solution containing no nitrogen would liberate nitrogenous matter in the solution in appreciable quantities. The flask used for this purpose was pea flask no. 1302, in which the nutrient solution was composed of 1.5 grams KH_2PO_4, 1 gram $CaCl_2$, 0.07 gram Na_2SO_4, and 0.5 gram $Fe_2(PO_4)_2 + 8H_2O$; the flask was then filled with sterile tap water, the $Fe_2(PO_4)_2 + 8H_2O$ remaining largely undissolved.

After the contents of the flasks were sterilized and the young plants transferred, the cultures were taken to the greenhouse, where they remained for various periods. It was not intended to make any systematic study of the relation of the stage of growth to the quantity of organic nitrogen in the solution at harvest. This would have been impossible under the circumstances, for the plants were set out at different times and, since conditions affecting plant growth vary greatly in the greenhouse at different seasons of the year, no comparison of this kind could be attempted. The same difficulty would obtain in case a comparison of different plants was desired, except in the case of such plants as were placed in the greenhouse at about the same time.

When it was decided to harvest a plant, the flask was brought to the laboratory, and, after a photograph had been taken, the plant was removed from the nutrient solution and the dry matter and nitrogen were determined in the entire plant including the roots. A plating of the nutrient solution was made to determine whether the solution was sterile. The presence of any molds or bacteria thus detected excluded from the experiment the flask so contaminated.

The volume of liquid remaining in the flask was measured, and determinations were made of the nitrate nitrogen remaining in the solution, the ammonia nitrogen, if any, and the organic nitrogen present in soluble form. The deposit at the bottom of the flask was collected and a determination was made of the organic nitrogen contained in it. The reason for ascertaining the quantity of nitrate nitrogen remaining in the solution was merely to observe whether the presence or absence of this form of nitrogen affected the liberation of organic nitrogen by the plant.

A small quantity of nitrogen was contained in the germinated seed and plantlet placed in the flask, but there was no way by which this nitrogen

TABLE 1. FORMS AND AMOUNTS OF NITROGEN PRESENT IN SOLUTIONS IN WHICH PLANTS HAD GROWN

Kind of plant	Maize	Oat	Pea	Pea*	Maize	Vetch
Serial no.	1259	1272	1280	1302	1303	1308
Date of setting plant in flask	Dec. 1	Dec. 29	Dec. 9	Dec. 9	Dec. 1	Jan. 20
Date of removing plant from flask	April 1	April 11	April 26	April 26	June 7	June 12
Growing period (days)	122	105	139	139	189	144
Dry matter in plant (milligrams)	11,367.8	4,089 0	6,823 0	.....	48,490 0	18,050 0
Nitrogen in plant (milligrams)	248 9	151 0	231 5	43 6	472.3	344 9
Volume of solution at harvest (cubic centimeters)	9,850 0	7,320 0	4,510 0	6,815 0	6,950 0	2,290 0
Condition of solution	Sterile	Sterile	Sterile	*B. radicicola*	Sterile	Sterile
Nitrogen in solution at harvest in form of						
NO_3 (milligrams)	241 9	198 3	89 6	None	None	None
NH_3 (milligrams)	2 7	Trace	Trace	2 0	6 3	None
Organic matter (milligrams)	13 4	18 3	3 6	2.0	3.4	4.4
Organic nitrogen in deposit at bottom of flask (milligrams)	0 8	0 5	0 2	0.7	0.6	1 0

* The nutrient solution in which this pea plant was grown contained no combined nitrogen at the beginning of the experiment.

could be transferred to the nutrient solution except thru the roots, as the seed did not come in contact with the solution at any time.

The data for this experiment are presented in table 1. The figures give some definite information regarding the presence of organic nitrogen in the substratum in which these plants grew and which contained only inorganic nitrogen at the time when the young plants were set out. Of the plants used — oats, peas, maize, and vetch — all liberated organic nitrogen, which was found both in the solution and in the deposit at the bottom of the flasks. The quantity of organic nitrogen in the solution was always several times as much as that in the deposit.

The organic nitrogen in the deposit at the bottom of the flasks is probably the result of sloughing off of the root cells, as is indicated by the presence of plates of cells in the deposit. It is possible also that a part, at least, of the nitrogen in solution is liberated from the plant cells in the same way. There is no direct evidence that the nitrogenous matter is liberated in any other way, but it is perhaps questionable whether the quantity found in solution, especially during the early stages of growth, could all have come from detached cells. That these cells are alive and remain so for a considerable time has been noted by Knudson (1919).

Organic nitrogen appeared in the solution before the nitrates were all removed. It is evident that organic nitrogen is liberated by these plants in the early stages of their growth and not exclusively at the period between full bloom and maturity. That only the loss of nitrogen in later growth was noticed in the field experiments previously reviewed was doubtless due to the fact that the plants were absorbing little nitrogen at that stage and were liberating it more rapidly than they were absorbing it.

The quantity of organic nitrogen liberated under field conditions may not correspond to that obtained in these experiments, as under the conditions of the experiments there was no removal of organic matter by organisms other than the plant, while in the field there would presumably be conversion of the organic nitrogen into ammonia and nitrates.

The pea plant that grew in a solution without the addition of combined nitrogen, liberated organic nitrogen into the solution in which it grew. The growth was by no means as vigorous as that of the pea plant which was furnished with nitrate nitrogen, and the plant itself contained only about one-fifth as much nitrogen as did the other pea plant, but it liberated more than half as much organic nitrogen.

ORGANIC NITROGEN PRESENT IN NUTRIENT SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

In order to ascertain how the stage of growth of maize plants affects the quantity of organic nitrogen found in the nutrient media, a series of flasks containing nutrient solution were prepared in the usual way and a young plant was set in each flask. The flasks were placed in the greenhouse on December 24, 1915. They were allowed to remain there until the time when they were to be brought to the laboratory for analysis of the plants and the contents of the flasks. The first flask was opened on March 4, 1916, and the others were opened at intervals of a number of days until May 24, 1916, when the last one was opened. The interval between the opening of the first and that of the last flask covers a period of growth between the pre-tassel stage and maturity (figs. 5 to 9).

The maize plants grew well and most of those that were old enough at harvest bore ears. The variety used was a pop corn which under normal conditions does not grow very tall. Data regarding all of the flasks the contents of which were sterile at harvest are given in table 2. All of the contaminated flasks except one were discarded in presenting the results. The one exception was made because it fell in what would otherwise have been a wide interval between the dates of harvest. It also represented the condition of most of the contaminated flasks, which did not appear to be materially different from the sterile flasks in respect to the quantity of organic nitrogen present in the nutrient solution.

The data in table 2 are consistent in showing the presence of organic nitrogen in all solutions in which plants grew. This organic nitrogen appeared at all stages in the growth of the plants, but there seemed to be a tendency for it to decrease in amount with progressive stages in the life of the plant, and especially about the time when the plant approached maturity, at which stage there was a very decided falling off in the quantity present.

The organic nitrogen in the deposit at the bottom of the flask did not show any decided tendency to vary in amount with the successive stages of plant growth. The amount present was uniformly smaller than that in the solution. In the bottom of the flask there could usually be found plant cells, indicating the sloughing off of root caps and root hairs. This suggests a possible source of at least a part of the organic nitrogen in

FIG. 5. MAIZE PLANT 71 DAYS OLD
(Table 2, serial no. 1246)

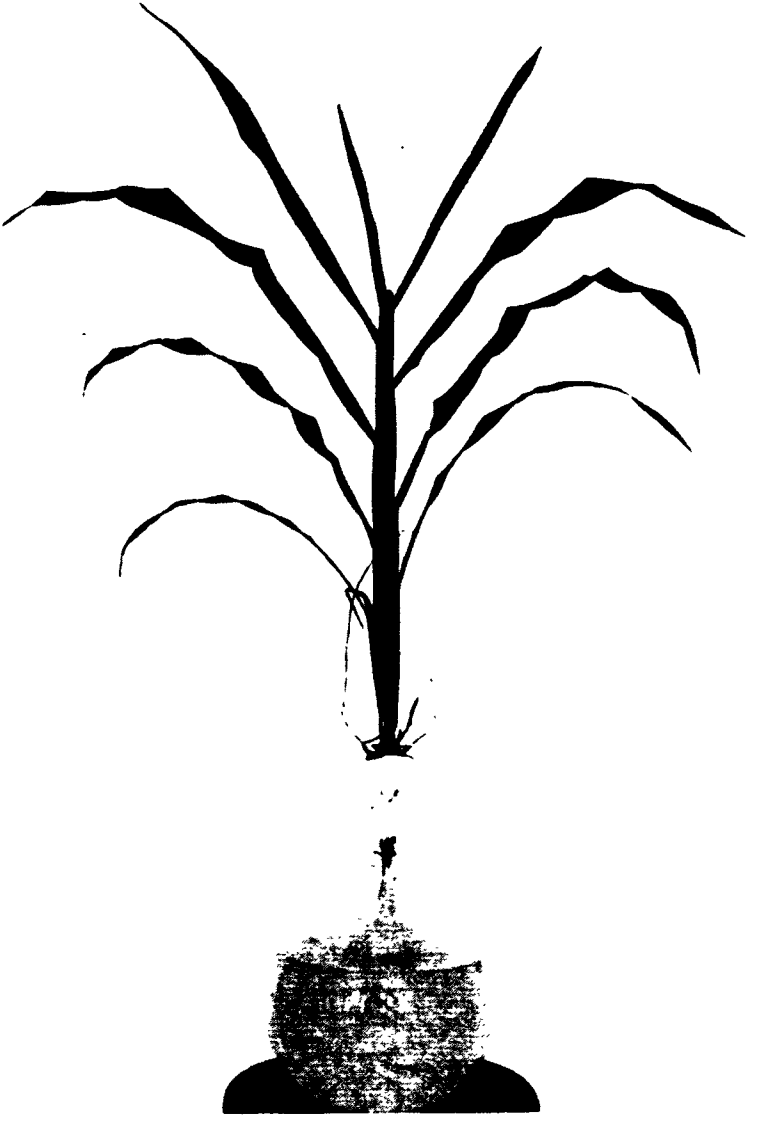

FIG. 6. MAIZE PLANT 82 DAYS OLD
(Table 2, serial no. 1250)

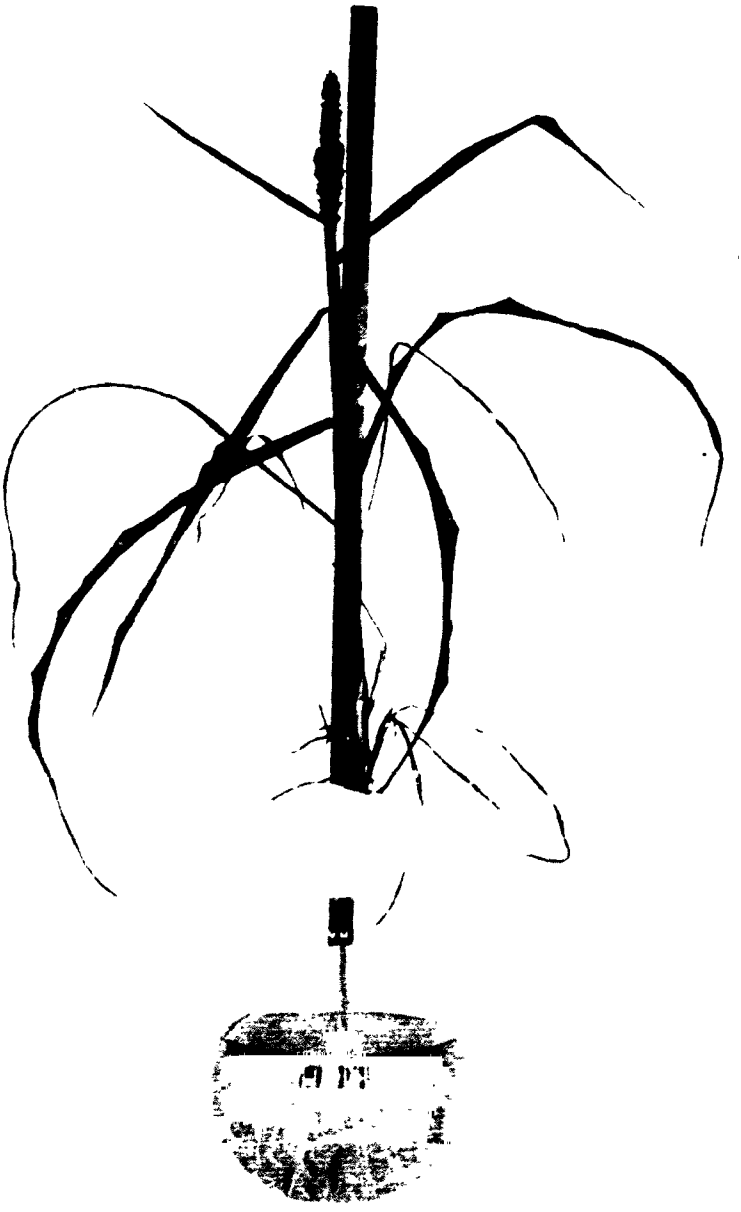

FIG. 7. MAIZE PLANT 91 DAYS OLD
(Table 2, serial no 1253

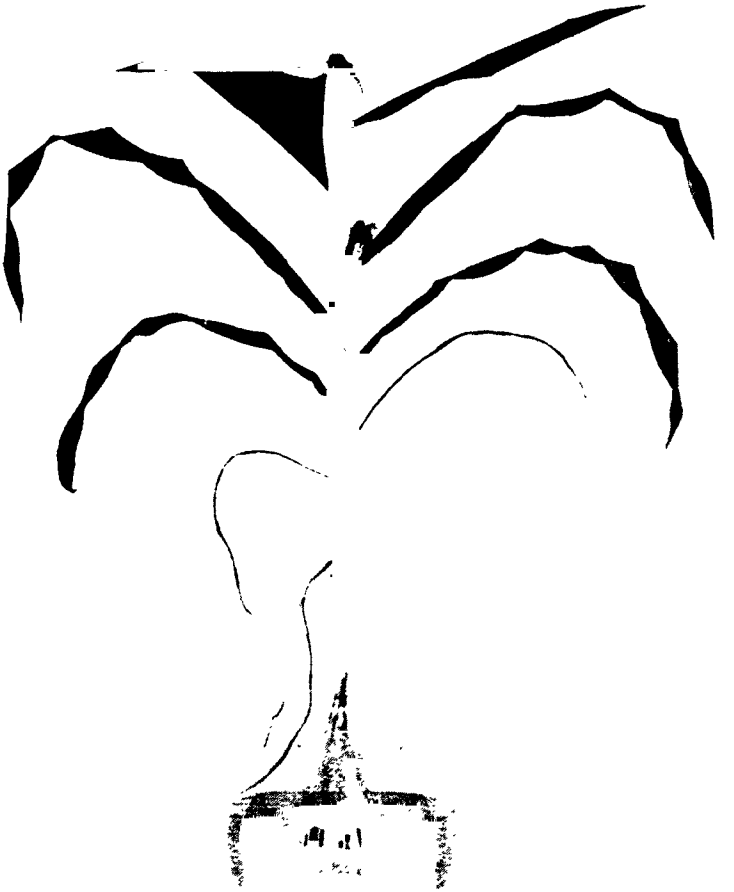

FIG. 8. MAIZE PLANT 96 DAYS OLD
(Table 2, serial no. 1256)

solution and in the deposit, but whether it would account for all of the former may be questioned.

It was when the solution remaining in the flask was reduced to a rather small volume that the quantity of organic nitrogen in the solution fell decidedly. However, it did not appear that this was due to the saturation of the solution, as the large flask no. 1291, which contained 3700 cubic centimeters of solution at harvest, had no more organic nitrogen in the solution than did the smaller flask no. 1286, which contained only 1500 cubic centimeters of solution when opened.

It seems likely that the organic nitrogenous compounds are absorbed by the plant as it approaches maturity. This may be in order to establish equilibrium between the plant juices and the solution in which the roots are immersed. In the soil there would probably be a tendency for these organic nitrogenous compounds to undergo ammonification and nitrification, and, if conditions are favorable for these processes, there might be very little organic nitrogen in the soil solution at any time. Consequently, if there is a tendency to establish osmotic equilibrium there would probably be a much greater removal of organic nitrogen from a plant growing in soil than from one growing in a sterile solution.

Organic nitrogen appears in the nutrient solution before all of the nitrate nitrogen has disappeared, but the disappearance of nitrates is not a signal for the decided drop in organic nitrogen which occurs much later.

Previous investigations concerning the liberation of nitrogen from higher plants during growth have been conducted in two ways One of these consisted in analyzing the plants from a measured area of land at certain intervals in the growth of the plants. Such experiments usually demonstrated that there was a loss of nitrogen from the plants between blossoming and ripening. Owing to the fact that the plants were absorbing nitrogen rapidly at earlier stages of growth, the income was greater than the outgo and consequently the earlier movement of nitrogen was not discovered. The other method, used by Le Clerc and Breazeale, in which the leaves were washed, showed a removal of nitrogen at each stage at which it was applied, but naturally the loss so occasioned would be rather small under natural conditions as it would occur only during periods of rainfall or heavy dew.

The movement of organic nitrogen from the plant into the soil solution would presumably be considerable, and possibly the cycle involving the absorption of nitrate nitrogen by the plant and its conversion into organic compounds followed by a return to the soil of a part of these compounds and a reconversion of the nitrogen into nitrates may be a very extensive one. What part it may play in the economy of the plant is at present only a matter of speculation. It may be that the liberation of this material is merely casual, while, on the other hand, it is conceivable that the substances so eliminated are more or less injurious to the plant and when exposed to the decomposing bacteria of the soil are destroyed and not reabsorbed. When liberated into a sterile solution they are not destroyed, and, being largely reabsorbed, they may exert a toxic effect on the plant, which never makes a perfectly healthy growth in these solutions even when it produces grain.

TOTAL ORGANIC MATTER PRESENT IN NUTRIENT SOLUTIONS IN WHICH MAIZE PLANTS HAD GROWN

The experiments previously described have dealt only with the forms of nitrogen present in solutions in which higher plants have grown. It would appear to be a matter of some interest to know something of the total quantity of organic matter in these solutions, and what proportion this organic matter may bear to the nitrogen present. For this purpose a number of flasks containing the usual nutrient solution of one-tenth strength were prepared and maize plants were grown in these in the customary way. It was planned to have a set of four flasks to be opened after the plants had grown for about two months, and another set of the same number of plants to be harvested when fully mature. Unfortunately, the flasks in the latter set were all found to be contaminated when opened, and for that reason the data furnished by these flasks are not considered to be of value and are not included in table 3, which gives the data for the first four flasks only:

TABLE 3. TOTAL ORGANIC MATTER AND NITROGEN PRESENT IN SOLUTIONS IN WHICH MAIZE PLANTS HAD GROWN

Kind of plant	Maize	Maize	Maize	Maize
Serial no	1	2	3	4
Date of setting plant in flask	May 1	May 1	May 1	May 1
Date of removing plant from flask	June 23	June 23	June 23	June 23
Growing period (days)	53	53	53	53
Dry matter in plant (milligrams)	17,266.4	23,076 4	24,058.5	20,443 0
Nitrogen in plant (milligrams)	357.1	327.4	400 0	365.8
Volume of solution at harvest (cubic centimeters)	5,875 0	4,155 0	3,855 0	4,870 0
Condition of solution	Sterile	Sterile	Sterile	Sterile
Total organic matter in solution at harvest (milligrams)	466.6	353.1	476 1	535 7
Nitrogen in solution at harvest in form of				
NO_3 (milligrams)	0.0	0 0	0.0	0 0
NH_3 (milligrams)	0 0	0 0	0 0	0 0
Organic matter (milligrams)	1 7	1.0	1 3	1.4
Ratio of organic matter in solution to dry matter in plant	1:37 0	1:65 3	1:50 5	1:38 1
Organic nitrogen in deposit (milligrams)	0 0	0 4	0 8	0 6
Nitrogen in organic matter in solution (per cent)	0 35	0 27	0.27	0 27

The plants used in this experiment made a rather rapid growth, the conditions in the greenhouse during May and June being very favorable for the growth of maize. Not only had all of the nitrate and ammonia nitrogen disappeared from the solution, but the organic nitrogen had been reduced to a very small quantity, being, in fact, lower than in any of the other experiments of this kind. It was rather surprising under the circumstances to find so much total organic matter in the solution. Evidently but a small proportion of the organic matter present was of a nitrogenous character, as the percentage of nitrogen in the organic matter in solution is only about 0.3. Probably there was much carbohydrate material present. Knudson's (1920) investigations led him to conclude that reducing sugars are excreted by plant roots. Calculating the nitrogenous organic matter at 6.25 times the nitrogen present, such material would constitute only about one-fifth of the total organic matter. It is altogether likely that the proportion of nitrogen in the organic matter varies at different stages in the growth of the plant.

The ratio of the organic matter in the solution to the dry matter in the plant is surprisingly high. This varied from one part in the solution to

37 parts in the plant, which was the narrowest ratio, to one part in the solution to 65.3 parts in the plant, which was the widest ratio. If it is to be assumed that the decomposition of this organic matter in the soil would increase its liberation by the plant, the result would be that a very large quantity of organic matter would be transferred to the soil. It is entirely conceivable that higher plants may influence bacterial activity in the soil by means of this liberation of organic matter, which would furnish a source of energy for certain bacteria, as, for instance, nitrate consumers.

In the solutions in which these four plants grew there were at harvest no ammonia, no nitrates, and very little organic nitrogen, which condition indicates a strong demand for nitrogen by the plants. Sometimes ammoniacal nitrogen was found to be present in the solutions and sometimes it was absent. The cause of its formation is an unsolved problem. Two possibilities present themselves. One is that ammonification of the organic matter in the solution took place between the time when the flask was opened and the time when the test for ammonia was made, contamination of the solution from outside occurring after the flask was opened. This was guarded against as far as possible. Another hypothesis is that ammonia formation was due to enzymic action, the plants having liberated the necessary enzymes.

Possibly ammonia is commonly formed and when the demand of the plants for nitrogen is great it is absorbed and thus disappears from the solution. If it is derived from the liberated organic nitrogen, as seems possible, it may be the means by which organic nitrogen is rendered available to higher plants.

In a previous experiment, flasks were opened at four different stages in the growth of maize. As the periods of growth varied from a rather early stage, before the nitrate nitrogen was all removed from the solution, to maturity, it would have been a very interesting experiment had it not been for the fact that the last two flasks opened were found to be contaminated. The data, however, are all tabulated in table 4, altho there is, of course, no assurance that the results were not materially affected by the organisms that had gained access to the solutions.

The sterile flasks in this experiment agree with those in the experiment recorded in table 3 in showing the presence of a large amount of organic matter in the solution in which the plants grew. The amount was less

for the data shown in table 4, but the growth of the maize plants in the sterile flasks also was less. The quantity of inorganic matter and of organic matter appears to decrease and increase at the same periods if credence is to be given to the data from the last two flasks opened. The

TABLE 4. TOTAL ORGANIC MATTER AND NITROGEN PRESENT IN SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

Kind of plant	Maize	Maize	Maize	Maize
Serial no.	1	2	3	4
Date of setting plant in flask	June 28	June 28	June 28	June 28
Date of removing plant from flask	Aug. 3	Aug. 16	Aug. 30	Sept. 20
Growing period (days)	36	49	63	84
Dry matter in plant (milligrams)	10,200 0	24,100 0	32,200 0	65,000 0
Volume of solution at harvest (cubic centimeters)	6,200 0	6,950 0	2,850 0	2,790 0
Condition of solution	Sterile	Sterile	Contaminated	Molds
Nitrogen as nitrates in solution (milligrams)	32 4	Trace	0 0	0 0
Inorganic matter in solution (milligrams)	1,333 0	1,056 4	310 6	460 3
Organic matter in solution (milligrams)	291 4	284 9	76 9	251 1

data for inorganic matter were probably not influenced by the infection of flask no. 3, and this shows a gradual decrease in amount up to the sixty-third day of growth and then an increase at maturity, indicating a liberation of salts from the plant. Such liberation must, of course, have been by way of the roots. Admitting, then, that inorganic matter may be removed by the action of rainfall on the leaves, of which the investigations of Le Clerc and Breazeale leave little doubt, there appear to be at least two means by which this material may be liberated by the plant.

REDUCING AND OXIDIZING SUBSTANCES LIBERATED BY PLANT ROOTS

While many investigations have been made of the oxidizing and reducing enzymes in plants, very few have been undertaken for the purpose of ascertaining whether any of these bodies appear in the substratum in which the roots of plants are immersed. It was thought that the sterile solutions used in the experiments described above, in which plants of different kinds and of different stages of growth were produced, would permit of a series of tests for these substances under conditions that would exclude contamination from the seed or from outside sources,

and that these tests might possibly afford some information regarding the relation of the stage of growth of the plants to the presence of oxidizing or reducing substances.

REVIEW OF LITERATURE

Apparently the only examinations designed to detect the presence of reducing substances in media in which plants grew were those conducted by Schreiner and Sullivan (1910), who placed the roots, and in some cases the seeds also, of wheat seedlings in solutions of various reagents commonly used for detecting the presence of reducing substances. Considering only the tests in which roots alone were introduced into the reagent solution, these authors obtained reactions with starch-iodide solution, sodium selenite, and sodium tellurite. Tests for reduction of nitrates appear to have been made only where the seeds were present, and under these conditions nitrites were found by means of the Griess reaction. The seeds from which the seedlings were germinated had previously been treated with a 0.1-per-cent solution of mercuric chloride. The solutions in which the plants grew were not shown to be sterile.

It is well known that oxidizing enzymes occur within plant tissues and they are believed to play an important part in physiological processes. They have been found also in soils, but this does not furnish any proof that they are liberated by plant roots altho it suggests such a possibility. The presence in soils of large numbers of bacteria many of which are known to secrete enzymes, may well account for the appearance in soils of oxidizing enzymes without any contribution from roots of higher plants. It is equally true that the occurrence of enzymes within the plant would not necessarily lead to the conclusion that they are thus conveyed to the soil.

Not many investigators have taken up studies concerning the liberation of oxidizing substances by plant roots. The work of Molisch, Czapek, and Raciborski has been reviewed by Schreiner and Reed (1909), and hence it is not necessary to review it here. Schreiner and Reed, in the paper referred to, state that they have been able to detect the presence of oxidizing enzymes on certain parts of the surface of wheat roots. For this purpose they used alpha-naphthylamine, benzidine, vanillin, vanillic acid, phenolphthalin, aloin, and leuco-rosolic acid. As in their experiments for the detection of reducing substances, there was no evidence offered

to show that the solutions were sterile, but the authors state that it is improbable that the enzymes were produced by bacteria.

Summarizing the experiments to determine the presence of oxidizing enzymes outside of the growing roots of plants, it may be said that Molisch, Raciborski, and Schreiner and Reed report the finding of these enzymes and consider them to have been excreted by the roots as a normal condition of their growth. Evidence of the liberation of reducing substances is less conclusive, but if oxidizing enzymes are liberated by plant roots it is easily conceivable that reducing substances would be also, as both are well known to occur within the plant tissues.

TESTS FOR REDUCING AND OXIDIZING SUBSTANCES LIBERATED BY PLANT ROOTS

The data already presented show that a comparatively large amount of soluble organic matter may be given off by plant roots during the growing period. This organic matter may be derived in part from root caps and root hairs that are sloughed off by plant roots as development proceeds. The roots or detached cells may give up to the surrounding medium certain specific compounds, some of which may be enzymic in character. In order to obtain information on this subject a number of tests were made to detect the presence of certain substances that might influence reduction or oxidation.

Reducing substances

A number of reagents that had been proposed for the detection of the presence of reducing substances were used for testing the solutions in which maize plants had grown, and at the same time for testing check solutions consisting of the nutrient solution made up as it was for the growth of the maize plants. In some cases the solutions in which the plants had grown were boiled before being tested, but an unboiled portion was always tested at the same time. Some of the reagents failed to give a reaction with any of the solutions tested and were discarded. These were methylene blue, methyl violet, gentian violet, sodium selenite, and sodium tellurite. These failures may mean merely that the conditions under which their reactions occur did not obtain altho reducing substances may have been present.

Tests for reducing substances were made with prussian blue in solutions from six sterile flasks in which maize plants had grown, using both the unboiled and the boiled samples of the solutions as well as check nutrient solutions. These tests were made in solutions taken from plants at different stages of growth. Ten cubic centimeters of each solution was used, and each received two drops of a 0.5-per-cent solution of phenol. After the prussian blue was added, the tubes containing the solutions were allowed to stand for twenty-four hours, at the end of which time notes were taken on the results. In each of the six tests the unboiled solution in which the plant had grown gave a distinct reaction for reducing substances. The boiled solution gave no reaction in three tests, while in the other three the result was rather uncertain. The check solution gave no definite test for reducing substances.

Reduction of nitrates.— Since traces of ammonia were found in the sterile solution which had surrounded the maize roots, it was thought possible that thru the action of enzymes liberated by the plant this ammonia might have been formed from the nitrates in the nutrient solution. Tests for nitrates were made, using sulfanilic acid and naphthylamine acetate. No positive results were obtained. As a further test the diphenylamine reagent was employed. This reagent is considered to be positive to nitrite 1 part in 32,000,000 and to nitrate 1 part in 44,000,000. The tests were made with a series of sixteen flasks and no positive results were obtained.

This does not necessarily show, however, that reducing enzymes might not have been present, for the maize removed all the nitrates from the nutrient solution rather early in its development, and the liberation of reducing substances may not occur until after the plant has taken up most of the nutrients necessary for its development, or the nitrites may be absorbed by the plant.

The nitrites might not have been present because there were no nitrates from which they could be formed. The problem of supplying the nitrates and making the nitrite test was conducted as follows: Check flasks, twelve in number, were prepared with the same nutrient solution that was used for growing plants. A like number of test flasks were used which contained solution from around the plant roots. One hundred cubic centimeters was used in each flask, and the nitrate content was made equal in both check and test flasks. The flasks received phenol

to make the concentration 1 to 500, and were placed in the incubator at 23° C. The next morning tests were made for nitrites, using the Griess reagent. No visible differences were apparent. A second test for nitrites was made after forty-eight hours. The result was positive in every case. This test was repeated with the solution from another flask in which a maize plant had grown. While not so striking, the results in this case were also positive. Some tests were negative. A difference of NO_3 readings was not detectable in a colorimeter.

Another series of tests for nitrate reduction was conducted, using 5 cubic centimeters of the solutions in which maize plants had grown for periods of varying lengths and adding to this a small quantity of calcium nitrate solution, at the same time introducing two drops of a 0.5-per-cent solution of phenol. Alpha-napthylamine and sulfanilic acid were used to test for the presence of nitrites, the solutions being allowed to stand for certain lengths of time varying from two hours to three days. Such tests were made of the sterile solutions from eight flasks in which plants had been grown, the solutions being taken for the tests within a few minutes after the flasks were opened. A sample of the solution from each of the flasks except one was boiled before being tested, and another sample was not so treated. The check nutrient solution was tested in each case. Of the eight flasks tested, the unboiled solutions showed the presence of nitrites in every case but one, the check solution showed the absence of nitrites in six cases out of eight, and the boiled solution gave a reaction for nitrites in six tests but did not color so rapidly as did the unboiled. Apparently nitrate-reducing substances were usually present in the unboiled solutions in which the maize plants had grown, and boiling the solutions failed to render these substances incapable of bringing about reduction of nitrates in the presence of phenol.

While the process of boiling did not completely prevent the liquid surrounding the plant roots from effecting reduction of nitrates, it seemed to curtail its activity, as is indicated by the slower coloration of the reaction with the alpha-napthylamine and sulfanilic acid. The tests for reducing substances by means of prussian blue, on the other hand, did not give any more reaction with the boiled solutions than with the checks. While, therefore, the operation of boiling produced some effects corresponding to what might be expected from enzymes, there is some question as to

whether the reducing substances were of that nature in view of the results with reduction of nitrates.

Oxidizing substances

Peroxidases were detected in the culture solution in which the roots of maize, vetch, oats, peas, soybeans, alfalfa, and timothy had grown. From 8 to 10 cubic centimeters of each solution was placed in a dry test tube together with a few drops of hydrogen peroxide. This was allowed to stand for from two to three minutes, and then from two to three drops of a 5-per-cent phenol solution were added. The latter was then followed by an alcoholic solution of guaiac. It was considered that a positive test was recorded if the color became blue in thirty minutes. With this test no difficulty was experienced in obtaining a reaction with solutions from all of the flasks tested. Boiled solutions treated likewise gave no reactions.

In working with the solution in which vetch roots had grown, a very strong reaction was obtained by the use of hydrogen peroxide and phenol. The solution was placed in dry test tubes and a few drops of hydrogen peroxide were added. This was allowed to stand at room temperature. After from three to four minutes a few drops of a 5-per-cent phenol solution were run down the side of the test tube. Shortly after contact of the materials, a growing yellow color developed, which gradually increased and on long standing settled out. This test was negative when the same solution was boiled. An extract of macerated vetch roots and nodules gave the same test. If this material was boiled, however, no reaction was obtained.

Phenolpthalin was used as a reagent for indicating the presence of oxidizing substances in the solutions in which maize plants had grown. For these tests both boiled and unboiled samples of the solutions were used. Checks consisting of the nutrient solution in which no plants had grown were also included. Phenol was added, as in the previous tests. Results from these tests were usually negative.

Experiments in which guaiac were used without a peroxide indicated the presence of an oxidase in solutions in which maize plants had grown only when the plants were very young. Agar in which timothy plants were grown always gave a reaction with guaiac.

Tests with pyrogallol included only one sterile flask. No phenol was used. At the end of one-half hour the boiled solution was clear, the

unboiled was brown, and the check was a light yellow. On the whole the tests for oxidizing substances cannot be said to have offered very strong evidence of their presence except in the case of peroxidases.

Possible coexistence of oxidizing and reducing substances

Altho the number of tests for oxidizing enzymes were rather few, reactions indicating their presence were confined mainly to the solutions from flasks which gave no marked response to tests for reducing substances. It seems likely that both classes of substances are coexistent in solutions in which plants are growing, and that at one time the oxidizing substances may be dominant and at another the reducing substances. Differences in the intensities of the reactions at various times may thus be accounted for. Apparently with the maize plant the predominating reaction was for reducing substances thruout most of the stages of growth.

It would appear from these experiments that some form of reducing substance is always present in the solutions in which plants are growing. Whether oxidizing substances are always present, it is more difficult to say. They were found in some of the solutions taken from flasks in which the plants had reached only an early stage of growth, and unless they are destroyed later on they must be present thruout the entire life of the plant. In the natural soil solution, enzymes might be destroyed and thus removed from active operation except when freshly liberated.

Nature of oxidizing and reducing substances

Boiling the solutions in which plants had grown completely terminated the activities of the oxidases, as was to be expected. It did not always have that effect on the reducing substances, especially the nitrate reducers. There would thus seem to be considerable doubt as to whether the reducing substances were enzymic in character, but they at least had the power of bringing about reduction of nitrates in the absence of bacteria.

SUMMARY

Plants were grown with their roots in large flasks (8 or 12 liters capacity) containing a nutrient solution, the entire contents of the flasks being sterile. At various stages in the growth of the plants they were removed from the flasks and analyzed for nitrogen, and the nutrient solution was

tested for sterility and analyzed for nitrates, nitrites, ammonia, and organic nitrogen, and in some cases for total organic matter. A determination of organic nitrogen in the deposit at the bottom of the flasks was also made.

The plants grown were maize, oats, peas, and vetch. The nutrient solutions in which each of these plants grew contained nitrogen only in the form of nitrate when the plants were set in the flasks, but when the plants had grown for several weeks there was always organic nitrogen present. Even before the nitrate nitrogen had all been absorbed by the plants, organic nitrogen appeared in the solutions.

The deposit at the bottom of each flask contained a small quantity of organic nitrogen, which was probably derived from sloughing off of the root cells as indicated by the presence of plates of cells in the deposit. There was no direct evidence that the organic nitrogen in solution was liberated in any other way, but it is questionable whether such a large quantity could all come from these cells, especially during the early stages of growth.

A pea plant which grew in a solution without the addition of combined nitrogen liberated organic nitrogen into the solution in which it grew. The growth was by no means as vigorous as that of another pea plant which was furnished with nitrate nitrogen, and the plant itself contained only about one-fifth as much nitrogen as did the latter plant, but it liberated more than half as much organic nitrogen.

A series of flasks in which maize was growing were harvested at successive stages in the growth of that plant, and the plant and the flask contents were examined in the manner already described. Organic nitrogen appeared in the solutions at all stages in the growth of the plants, but there seemed to be a tendency for it to decrease in amount with progressive stages in the life of the plant and especially as the plant closely approached maturity. The organic nitrogen in the deposit at the bottom of the flasks did not show any decided tendency to vary in amount with the successive stages of plant growth.

Determinations of total organic matter were made in the solutions from some of the flasks. This constituent was very large in amount as compared with the nitrogenous organic matter present. Apparently there was much non-nitrogenous organic matter in the solutions. Calculating the nitrogenous organic matter at 6.25 times the nitrogen present,

this material would constitute only a small part of the total organic matter.

The presence of reducing substances in solutions in which plants had grown was indicated by certain tests, but a number of other reagents failed to give reactions. Nitrates were nearly always reduced in these solutions in the presence of an antiseptic. Boiling the solution did not entirely prevent nitrate reduction, but it greatly decreased the rate at which reduction proceeded.

Peroxidases were always present in solutions in which plants had grown. Boiling these solutions caused them to give no reaction for peroxidases. Tests for other oxidizing substances were not sufficiently satisfactory to warrant the conclusion that they were present.

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LYSIMETER EXPERIMENTS—II

RECORDS FOR TANKS 13 TO 16 DURING THE YEARS 1913 TO 1917 INCLUSIVE

LYSIMETER EXPERIMENTS—II

RECORDS FOR TANKS 13 TO 16 DURING THE YEARS 1913 TO 1917 INCLUSIVE

T. Lyttleton Lyon and James A. Bizzell

The object of the experiments herein described was, in the main, similar to that of the lysimeter experiments previously reported by the authors,[1] the essential differences being that a soil of another series was used, and that the effect of different cropping systems on the removal of the soil constituents in the drainage water was not a feature of the present experiment. The lysimeter tanks were like those described in the earlier publication.

THE SOIL USED

The tanks were filled in the summer of 1910 with a soil classified by the United States Bureau of Soils as Volusia silt loam. The soil is typical of much of the hill land of southern New York. It was formed, in the main, from shale and sandstone as the result of glaciation, which was rather feeble on these high lands. There is much broken shale distributed thru the soil, the pieces varying in size from small particles to large rocks. The subsoil is often very compact, and even on the hillsides poor drainage is the rule. The soil layer is often shallow on the hills, the shale in some places lying three or four feet below the surface.

In chemical composition this soil is distinguished by its low content of calcium. The other soil constituents are present in what may be considered fairly liberal quantities. Agriculturally Volusia silt loam ranks as poor, and the sample placed in these lysimeter tanks is considerably less productive than the average soil of the type. It is a much less productive soil than the Dunkirk clay loam contained in tanks 1 to 12. Its low productivity as a type may be due in part to its location, which is mainly on high elevations, the approaches to which are steep, making it inaccessible to railroads and thus adding to the difficulty of applying lime and fertilizers, which have consequently been meagerly used on these lands.

[1] Lyon, T. Lyttleton, and Bizzell, James A. Lysimeter experiments. Records for tanks 1 to 12 during the years 1910 to 1914 inclusive. Cornell Univ. Agr. Exp. Sta. Memoir 12: 11-15. 1918.

Acknowledgment — The authors wish to express their thanks to Mr. E. W. Leland for his services in measuring and sampling the drainage water during the entire period of the experiments, and for supervising the cultural operations on the tanks.

Volume weight

Before the soil was placed in the tanks all stones larger than a walnut were removed from it, but, as is characteristic of this soil series, a large number of small stones still remained. It is probably on this account that the volume weight of the soil was so high. The weight of each twelve-inch layer of air-dry soil placed in the tanks is shown in table 1:

TABLE 1. AVERAGE WEIGHT OF EACH TWELVE-INCH LAYER OF SOIL IN TANKS

	First foot (pounds)	Second foot (pounds)	Third foot (pounds)	Fourth foot (pounds)
Weight of soil in tanks	2,250	2,170	1,850	1,750
Weight of soil per acre	5,625,000	5,425,000	4,625,000	4,375,000

This, it may be remarked, is a soil having greater volume weight than the Dunkirk clay loam used in tanks 1 to 12 inclusive, owing, in part at least, to the large number of stones.

Mechanical composition

A statement of the mechanical analysis of the soil by the centrifugal method, including all particles from fine gravel to clay, is given in table 2:

TABLE 2. MECHANICAL COMPOSITION OF SOIL IN FIELD FROM WHICH TANKS 13 TO 16 WERE FILLED

Separates	First foot (per cent)	Second foot (per cent)	Third foot (per cent)	Fourth foot (per cent)
Fine gravel	2 32	5 32	3 00	1 14
Coarse sand	2 91	4 83	2 78	2 23
Medium sand	3 02	4 64	2 85	2 16
Fine sand	6 32	8 60	6 30	6 16
Very fine sand	15 92	18 22	15 80	11 79
Silt	50 88	42 60	51 25	39 91
Clay	18 63	16 79	18 02	26 61

This soil has always permitted the rainfall to percolate readily since it has been in the tanks. At no time has there been any stoppage and there has never been any water standing on the surface. The soil has, on the whole, drained more quickly and given a clearer percolate than did the Dunkirk clay loam in tanks 1 to 12.

Chemical composition

The samples used for the mechanical analysis of the soil in these tanks were taken from each foot layer and represent the average composition of the four tanks. The samples for the chemical analysis were obtained in the same manner. Bulk analyses were made. The methods used are stated in the appendix to Memoir 12 (pages 85 to 87) and the results are given in table 3:

TABLE 3. CHEMICAL ANALYSIS OF SOIL PLACED IN TANKS 13 TO 16

Constituents determined	First foot	Second foot	Third foot	Fourth foot
Nitrogen (per cent)	0 145	0 052	0 059	0 050
Organic carbon (per cent)	1 560	0 270	0 115	0 080
Calcium oxide (per cent)	0 230	0 165	0 260	0 365
Magnesium oxide (per cent)	0 560	0 390	0 290	0 460
Potassium oxide (per cent)	1 690	1 810	1 710	2 170
Sodium oxide (per cent)	1 120	0 940	0 810	1 070
Phosphoric anhydride (per cent)	0 071	0 039	0 018	0 071
Sulfur trioxide (per cent)	0 042	0 033	0 041	0 031
Carbon dioxide as carbonate (per cent)	0 030	0 030	0 020	Trace
Lime requirement (CaO in parts per million)	1,350	800	650	400

The chemical analysis shows a relatively good supply of plant nutrients as compared with the average soil or with the Dunkirk soil in tanks 1 to 12, but the Dunkirk is a much more productive soil, as is evident on comparison of the yields of crops from both sets of tanks. The only elements in which the surface foot of the Volusia soil is materially below that of the Dunkirk are calcium and sulfur. Nitrogen, phosphorus, and potassium are about equal in amount in the two surface soils. The lime requirement according to the Veitch method is somewhat greater in the Volusia soil. In the second, third, and fourth feet the calcium is

much higher in the Dunkirk soil. If the difference in productiveness and other properties is to be traced to any difference in chemical composition, it would appear that calcium and possibly sulfur are the only constituents that would call for inspection. It is true, however, that magnesium is higher in the surface foot of the Volusia soil.

MANURE AND FERTILIZERS USED

Farm manure was applied once to the soil in each of the four tanks. This application was made in the spring of 1914. The analysis of the manure is given in table 4. The method of analysis is described in the appendix to Memoir 12, pages 90 and 91.

TABLE 4. COMPOSITION OF FARM MANURE APPLIED TO THE SOIL IN TANKS 13 TO 16

Constituents	Percentage composition	Pounds per acre
Dry matter....	21 26	4,252
Nitrogen	0 50	100
Phosphoric anhydride	0 37	74
Potassium oxide	0 36	72
Calcium oxide	0 63	126
Magnesium oxide	0 27	54

The burnt lime, of which one application was made, contained 91.95 per cent of CaO and a trace only of MgO.

METHODS FOR CHEMICAL AND MECHANICAL ANALYSES

The methods used for the chemical analyses of the soil, crops, drainage water, rain water, manure, lime, and potassium sulfate, and for the mechanical analysis of the soil, are described in the appendix to Memoir 12, pages 85 to 91, inclusive.

SOIL TREATMENT AND CROPPING SYSTEM

The four tanks used in this experiment were all filled in the late summer of 1910. From that time until the spring of 1913 they were not treated in any way, but the drainage was collected, measured, and analyzed in

order to have a complete record of all constituents removed in the drainage water from the time when the soil samples were taken for analysis. Since the present report does not attempt to show the difference in the composition of the soil at a later period, but is rather a discussion of the effect of the application of burnt lime on the composition of the drainage water and the plant ash, the drainage for the period previous to May 1, 1913, is not considered.

Farm manure was applied to each of the four tanks in the spring of 1913, the application being at the rate of 10 tons to the acre. Burnt lime was applied to tanks 15 and 16 in the spring of 1913 at the rate of 3000 pounds to the acre.

Tanks 14 and 16 were never planted to any crop, and growth of vegetation on them was prevented by hoeing. In the year 1915, when maize was growing on tanks 13 and 15, the unplanted tanks were hoed at the same time and in the same way as were the tanks planted to maize; when other crops were growing on the planted tanks, the unplanted ones were merely scraped with a hoe. In each tank planted to maize there were eighteen maize plants. Seven rows of oats and the same number of rows of barley were sown in each tank planted to those crops. The barley was used to replace wheat, which had been sown in the previous autumn and had winterkilled. Canada peas were planted broadcast. All crops grew to maturity and produced seed, but it was evident that the soil was not a very productive one. The manure, lime, and crop treatments are shown in table 5:

TABLE 5. SOIL TREATMENT AND CROPS RAISED ON LYSIMETER TANKS 13 TO 16 DURING THE PERIOD FROM 1913 TO 1917

Tank	Soil treatment		Crops raised				
	Fertilizer	Lime	1913	1914	1915	1916	1917
13	Farm manure	None	Oats	Canada peas	Maize.	Oats	Barley
14	Farm manure	None.	None	None	None	None.	None
15	Farm manure	Burnt lime	Oats	Canada peas	Maize.	Oats	Barley
16	Farm manure	Burnt lime	None.	None.	None.	None.	None

not caused a greater percolation of water. The same was true of the application of lime to the Dunkirk soil in tanks 1 to 12, in the earlier experiments. While this may not mean that the lime did not flocculate the upper layer of soil with which it was incorporated, it has some significance so far as drainage is concerned, since it indicates that liming a soil of this kind would not result in facilitating the removal of water thru tile drains.

WATER UTILIZATION BY CROPS

The water utilization by crops on this soil was large for the amount of dry matter produced, both when calculated to the minimum transpiration ratio and by the evapo-transpiration ratio. The former was calculated by subtracting the drainage from the planted tanks from the drainage from the unplanted ones, and amounts to 451 pounds of water for every pound of dry matter in the crops raised during the five-years period. This appears in tabular form in table 8:

TABLE 8. MINIMUM TRANSPIRATION FOR ALL CROPS RAISED DURING FIVE-YEARS PERIOD

Tanks	Cropping treatment	Average annual percolation per tank (pounds)	Average annual production of dry matter per tank (pounds)
14, 16	Unplanted	2,462	
13, 15	Cropped	1,871	1,4
Minimum transpiration		591	
Minimum transpiration ratio		1.451	

Evapo-transpiration ratio

The evapo-transpiration ratio was calculated by subtracting the average percolation thru the planted tanks for the five-years period from the rainfall on the same area for the same period, and dividing this by the number of grams of dry matter per tank in the crops produced. This ratio is given in table 9:

TABLE 9. EVAPO-TRANSPIRATION FOR ALL CROPS RAISED DURING FIVE-YEARS PERIOD

	Liters per tank
Rainfall (average annual)	1,388 7
Percolation from planted tanks (average annual)	848 7
Transpiration and evaporation from planted tanks	540 0
Evapo-transpiration ratio	1 908

Neither the minimum transpiration ratio nor the evapo-transpiration ratio is necessarily the same as the actual transpiration ratio. The former is likely to be less because the evaporation from the unplanted soil is almost always greater than the evaporation from the planted soil, and the latter is almost sure to be greater because it includes the water that evaporates from the surface of the soil as well as that which is transpired by the plants. The actual transpiration ratio therefore lies between 1:451 and 1:908.

It is significant that both transpiration ratios for the Volusia soil are so much wider than those for the Dunkirk soil, the former being about 56 per cent wider than the latter in both cases. It seems fair to assume that the actual transpiration ratio is correspondingly wider for the Volusia soil. Such differences cannot be attributed to conditions other than the soil, and probably arise from a difference in the concentration of the soil solution. The transpiration ratios are inversely proportional to the concentration of the drainage water and the crop yields from these two soils, as may be seen in table 10, the data in which are for the five-years periods already reported with the exception of the crop yields, which are for 1915, 1916, and 1917 only, since those were the only years in which the same crops were grown on both sets of tanks.

an important factor in crop production; on the other hand, it may be significant, especially if it is supported by evidence drawn from the removal of nitrogen in the drainage water.

Effect of liming on removal of nitrogen in drainage water

The quantities of nitrate nitrogen removed in the drainage water of unplanted soil afford a better means of ascertaining whether liming increases nitrate formation than does the removal of nitrogen in crops The data by years for the nitrogen in drainage water from unplanted soil are presented in table 13:

TABLE 13. NITROGEN IN DRAINAGE WATER OF UNPLANTED TANKS, CALCULATED TO POUNDS PER ACRE BY YEARLY PERIODS (MAY 1 TO APRIL 30)

Tank	Fertilizer	Burnt lime pounds	Nitrogen in drainage water (pounds per acre)					
			1913	1914	1915	1916	1917	Total
14.....	Manure.	None	73 41	34 21	49 31	34 47	38 71	230 11
16.....	Manure.	3,000	88 45	49.56	55 79	50 80	46.19	290 79

In each year the removal of nitrogen in the drainage water from the limed soil was greater than from the unlimed, which is very good evidence that the lime produced a condition more favorable to the production of nitrates. It may be remarked that the application of lime to the Dunkirk soil was not attended by any increase in the removal of nitrogen by the drainage water or by the crops. This difference in effect of lime is all the more striking inasmuch as the lime requirement of the surface foot of the Dunkirk soil is very little less than that of the Volusia. The percentage of calcium, however, is about one-third less in the surface foot of the Volusia. In this case the relative calcium content of the soil is a better guide to its need of lime for nitrification than is the lime requirement as determined by the Veitch method.

Effect of liming on removal of nitrogen in both drainage water and crops

While the nitrogen in the crops alone may not be an adequate guide to the effect of lime on the soil, the nitrogen in the crops added to that in the drainage water from the same tanks is perhaps somewhat more com-

prehensive. These data are given in table 14. It is apparent from this table that the application of lime to this soil results in an increased

TABLE 14. NITROGEN IN BOTH DRAINAGE WATER AND CROPS, CALCULATED TO POUNDS PER ACRE IN YEARLY PERIODS

Tank	Burnt lime (pounds)	Nitrogen in both drainage water and crops (pounds per acre)					
		Oats 1913	Peas 1914	Maize 1915	Oats 1916	Barley 1917	Total
13	None	46 03	74 47	44 78	26 96	23 51	215 75
15	3,000	57 46	114 16	51 67	28 81	28 10	280 20

removal of nitrogen in the combined crop and drainage water. There would seem to be little doubt, in view of the data presented in the last three tables, that the effect of lime on this soil is to increase nitrate formation.

RELATION OF DIFFERENT CROPS TO FORMATION OF NITRATES

It has been noted that the experiments with Dunkirk soil indicated certain rather definite relationships between certain kinds of plants and the formation of nitrates. A similar relationship appears to exist in the experiments with Volusia soil, as may be seen in the data given in table 15:

TABLE 15. AVAILABLE NITROGEN IN SOIL PRODUCING DIFFERENT CROPS, AS MEASURED BY THE NITROGEN OF THE CROP AND OF THE DRAINAGE WATER

(In pounds per acre)

Crop	Nitrogen in planted tanks (average of tanks 13 and 15)				Nitrogen in drainage water in bare tanks (average of tanks 14 and 16)	Excess (+) or deficiency (−) in planted tanks
	In drainage water	In tops	In roots*	Total		
Oats (1913)	16	35	12	63	81	−18
Peas (1914)	12	81	27	120	42	+78
Maize (1915)	15	32	11	58	52	+ 6
Oats (1916)	4	23	8	35	42	− 7
Barley (1917)	4	21	7	32	42	−10

*Estimated at one-third the quantity in tops.

Estimating the nitrogen in the roots of each crop to amount to one-third the quantity in the above-ground part, it will be seen that the nitrogen in the oat crop added to the nitrogen in the drainage water from the tanks on which that crop grew was less in amount than the nitrogen in the drainage water from the bare tanks for the same period. The same was true of barley, but it was not true of maize or of peas. The excess of nitrogen from the pea tanks can doubtless be ascribed to the nitrogen-fixing properties of *Bacillus radicicola* in the nodules of the pea roots. The excess nitrogen from the maize tanks must be ascribed to some different phenomenon. It has been suggested[3] that some plants have the property of depressing the formation of nitrates, and that certain plants possess this property to a greater degree than do others. The data here presented are in line with such an hypothesis.

REMOVAL OF CALCIUM

Calcium was removed in the drainage water to a much greater extent than was any other of the bases determined, but in relatively small amounts by the plants. A comparison of the calcium in the drainage water of the Dunkirk and Volusia soils shows that the latter lost more calcium by leaching than did the former, in spite of the fact that this soil contained only about two-thirds as much of that element as did the Dunkirk soil. On the other hand, the crops grown on the Volusia soil contained less calcium but the yield of crops was much smaller. The total removal of calcium from the Volusia soil, from both planted and unplanted tanks, was greater than that from the Dunkirk.

Effect of plant growth on removal of calcium

In the experiments with Dunkirk soil it was found that less calcium was removed from the planted soil in crop and drainage water combined than was found in the drainage alone from the unplanted soil. This is true also of the Volusia soil, as may be seen from table 16:

[3] Lyon, T. Lyttleton, and Bizzell, James A. Some relations of certain higher plants to the formation of nitrates in soils. Cornell Univ. Agr. Exp. Sta. Memoir 1: 111. 1913.

TABLE 16. AVERAGE ANNUAL REMOVAL OF CALCIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Calcium removed in		Total calcium removed
		Drainage water	Crops	
13, 15	Planted	256 4	8.7	265 1
14, 16	Bare	351 4		351 4
Calcium conserved by cropping				86 3

The process of cropping conserves the calcium in the soil even when the entire crop is removed. The reason for the greater removal of calcium from the uncropped soil may be found, in part at least, in the large formation and leaching of nitrates when plants are not present. In table 17 are shown the average quantities of nitrates found annually in the drainage water of the planted and the unplanted tanks.

TABLE 17. AVERAGE ANNUAL REMOVAL OF NITRATES IN DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tanks	Soil treatment	Nitrates removed (pounds per acre)
13, 15	Planted	47 0
14, 16	Bare	231 7

The nitrates in the drainage water from the cropped soil would account for only about 11.5 pounds of calcium, while the nitrates from the unplanted soil correspond to about 56.5 pounds of calcium which might be removed in the form of nitrate. This would still leave about 245 pounds of calcium that had been removed in the drainage water from the planted soil in some form other than nitrate, and about 285 pounds from the unplanted soil.

The concentration of calcium in the drainage water from the planted and from the unplanted soil shows little difference, but this is in the same order as its total removal. This may be seen in table 18, in which is stated in parts per million the average calcium content for the five-years period.

TABLE 18. AVERAGE CALCIUM CONTENT OF DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tank	Soil treatment		Calcium (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	52 3	54 4
15	Planted	Limed	56 6	
14	Bare	Not limed	49 9	58 0
16	Bare	Limed	68 0	

The greater loss of calcium from the unplanted soil was not due entirely to the greater percolation of water thru that soil, since in that case the concentration would not be greater. It would appear that the presence of a large amount of a strong acid, such as nitric acid, in the unplanted soil would explain the greater concentration of the calcium in the drainage water of that soil as compared with the weaker carbonic acid in the planted soil.

Effect of liming on removal of calcium

The application of burnt lime to the Dunkirk soil at the rate of 3000 pounds to the acre in the earlier experiments did not result in increasing the quantity of calcium in the drainage water or in the ash of the crops produced. A similar application to the Volusia soil in this experiment appears to have decreased the amount removed in both of these ways, as may be judged from the data presented in table 19:

TABLE 19. CALCIUM IN DRAINAGE WATER AND IN CROPS
(In pounds per acre, annual average)

Tank	Burnt lime (pounds)	Calcium in drainage water	Calcium in crops	Total calcium
13	None	257 6	7 46	265 1
14	None	319 4	. . .	319 4
15	3,000	255 1	10.09	265 2
16	3,000	383 4	. . . .	383 4

The figures for average annual calcium removal for the entire five-years period, as given in table 19, show a very large increase in the quantity of calcium leached out of the bare limed soil as compared with that from the bare soil unlimed; they show also a moderate increase in the calcium contained in the crops, but they do not indicate any effect from the liming on the calcium leached from the cropped soil. The evidence, however, is in favor of the conclusion that liming increases the amount of soluble calcium in Volusia soil, while it has no such effect on Dunkirk soil. This is hardly to be accounted for by the absorbent properties of the soil for lime, since Volusia soil has a somewhat higher lime requirement than Dunkirk as determined by the Veitch method.

The concentration of calcium was appreciably greater in the drainage from the limed soil than in that from the unlimed soil, both when planted and when kept free of vegetation, as may be seen in table 18.

Liming to maintain the calcium content

The Volusia soil, altho low in calcium, is annually losing a large quantity in the drainage water, particularly from the unplanted soil. The removal of calcium in the ash of crops has been small as compared with that in the drainage water. If the loss of calcium from the limed soil were to be replaced, it would require an annual application of 536 pounds of pure burnt lime, or 957 pounds of pure limestone, to supply the uncropped soil, and 371 pounds of burnt lime, or 662 pounds of limestone, to supply the planted soil with calcium to the amount removed in the crops and in the drainage water.

REMOVAL OF MAGNESIUM

Magnesium was removed in much smaller quantity than was calcium, both in the drainage water and in the crops. In both ways the removal was less from the Volusia soil than from the Dunkirk, altho the removal of calcium was greater.

Effect of plant growth on removal of magnesium

The effect of plant growth on the removal of magnesium is brought out by table 20. It will be seen that there is a greater loss of magnesium in

TABLE 20. AVERAGE ANNUAL REMOVAL OF MAGNESIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Magnesium removed in		Total magnesium removed
		Drainage water	Crops	
13, 15	Planted	30 6	3 5	34 1
14, 16	Bare	45.4	.....	45 4
Magnesium conserved by cropping				11 3

the drainage water of the uncropped soil than in both the drainage and the crops of the planted soil. The large quantity of magnesium leached from the bare soil is apparently caused mainly by the solvent action of the nitric acid, as was the case with calcium.

Not only is the total removal of magnesium greater from the bare than from the planted soil, but its concentration is greater in the water from the uncropped soil, as may be seen from table 21:

TABLE 21. AVERAGE MAGNESIUM CONTENT OF DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tank	Soil treatment		Magnesium (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	6.1	6.3
15	Planted	Limed	6.6	
14	Bare	Not limed	7.3	8.2
16	Bare	Limed	9.2	

Effect of liming on removal of magnesium

The effect of liming the soil was to increase the removal of magnesium both in the leachings and in the crops, as may be seen in table 22. There

TABLE 22. AVERAGE ANNUAL REMOVAL OF MAGNESIUM FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Magnesium removed from planted tanks			Tank	Magnesium leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	29.6	3.06	32.66	14	39.30
Limed	15	31.7	3.93	35.63	16	51.60

appears to be a basic exchange, similar to that which occurred in the Dunkirk soil, by which magnesium was liberated and dissolved by the soil water. The concentration of magnesium also was greater in the drainage water from the limed soil than in that from the unlimed, as may be seen in table 21.

REMOVAL OF POTASSIUM

Potassium differs from the other bases that were determined in the Dunkirk soil in that it was removed in greater quantities by the crops than by the drainage water. This was not true of the removal of potassium from the Volusia soil.

Effect of plant growth on removal of potassium

In spite of the fact that less potassium was removed by crops than by drainage water in these experiments, the total removal of potassium was greater from the planted than from the bare tanks. This is entirely contrary to the removal of calcium from the same tanks, as may be seen in table 23:

TABLE 23. AVERAGE ANNUAL REMOVAL OF POTASSIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Potassium removed in		Total potassium removed
		Drainage water	Crops	
13, 15	Planted	73 2	34 1	107
14, 16	Bare	84 5		84
Potassium conserved by not cropping				22

While the growth of crops conserved the calcium in the soil, the same operation increased the loss of potassium. There was little difference in the concentration of potassium in the drainage water from the planted and from the bare tanks, as is shown in table 24:

TABLE 24. AVERAGE POTASSIUM CONTENT OF DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tank	Soil treatment		Potassium in drainage water (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	18 3	15 9
15	Planted	Limed	13 6	
14	Bare	Not limed	15 5	14 0
16	Bare	Limed	12 5	

In respect to the concentration of potassium in the drainage water from the bare and from the planted tanks, the Volusia and the Dunkirk soils are in accord. It is probable that this is to be accounted for, in part at least, by the greater volume of percolate from the bare soil, but it seems possible that the plant growth effects a solvent action on the soil potassium which is indicated by the fact that the total removal of potassium in the crops and in the drainage combined is greater than that in the drainage from the bare soil.

Effect of liming on removal of potassium

The application of lime to this soil resulted in a decrease in the quantities of potassium contained in the drainage water and in the crops. This is shown in table 25:

TABLE 25. AVERAGE ANNUAL REMOVAL OF POTASSIUM FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Potassium removed from planted tanks			Tank	Potassium leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	88 6	35 08	123 68	14	99 1
Limed	15	57 8	33 12	90 92	16	69 9

There is nothing in this experiment to indicate that the application of lime caused the liberation of potassium. The same was true of the experiment with Dunkirk soil It may be remarked, however, that if the application of lime did liberate any potassium from the surface soil, it may have been absorbed by the lower layers of soil and thus have been removed from the drainage water

The concentration of the drainage water from the limed and from the unlimed soil does not give any more indication of the liberation of potassium than do the quantities removed. The concentration of potassium is stated in table 26:

TABLE 26. POTASSIUM CONTENT OF DRAINAGE WATER FROM LIMED AND FROM UNLIMED TANKS

Tank	Soil treatment		Potassium (parts per million)
	Crop	Lime	
13	Planted	Not limed	18.3
15	Planted	Limed	13 6
14	Bare	Not limed	15 5
16	Bare	Limed	12 5

REMOVAL OF SULFUR

Sulfur was recovered in the drainage water as sulfate, and it is significant that the years in which the content of sulfur in the drainage water was large were the years in which the removal of nitrogen by leaching was large. Drainage water from the Volusia soil contained somewhat less sulfur than did that from the Dunkirk, but the crops on the former soil contained as much sulfur as did those on the latter altho the yields were much smaller.

Effect of plant growth on removal of sulfur

There is one respect in which nitrogen and sulfur differ radically in this experiment, and that is in the proportion removed by crops and by drainage water, respectively. Nitrogen is removed most largely by the crops on planted soil, while sulfur is carried off mainly by the drainage water. The figures for sulfur in crops and in drainage water during the period of the experiment are given in table 27. The total quantity of

TABLE 27. SULFUR IN DRAINAGE WATER AND IN CROPS
(In pounds per acre, annual average)

Tank	Lime treatment	Sulfur in drainage water	Sulfur in crops	Total sulfur
13	Not limed	35 2	9 6	44
14	Not limed	43 3		43
15	Limed	33 7	10 7	44
16	Limed	39 0		39

sulfur removed from the planted tanks is not materially different from that removed from the bare tanks.

Effect of liming on removal of sulfur

In the experiments with Dunkirk soil the application of lime was accompanied by an increase in the quantity of sulfur in the drainage water. In the present experiments this was not the case, as may be seen in table 28:

TABLE 28. AVERAGE ANNUAL REMOVAL OF SULFUR FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Sulfur removed from planted tanks			Tank	Sulfur leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	35 2	9 6	44.8	14	43 3
Limed	15	33 7	10 7	44 4	16	39 0

Liming the Dunkirk soil did not result in an increased formation of nitrates but apparently favored sulfofication. Application of lime to the Volusia soil was accompanied by increased nitrification but had no effect on the production of sulfates. This would perhaps indicate that the conditions favorable to one of these fermentations are not always favorable to the other.

REMOVAL OF PHOSPHORUS

The Volusia soil, like the Dunkirk, has never furnished more than a trace of phosphorus in the drainage water. The data on removal of this element are therefore confined to the ash analyses of the crops. The average annual removal of phosphorus (calculated to the element P) is shown in table 29:

TABLE 29. PHOSPHORUS IN CROPS
(In pounds per acre, annual average)

Tank	Soil treatment	Phosphorus in crops
13 ..	Not limed.	9 36
15	Limed	11 12

There is a larger annual removal of phosphorus in the crops grown on the limed soil than in those from the unlimed soil. This was borne out by the data for each year, which are given in table 7 of the appendix (page 92). The year 1913 was the only one in which more phosphorus did not appear in the limed crops. In this respect there was no similarity between the Volusia and the Dunkirk soil, the latter having shown no increase in the quantity of phosphorus in the crops grown on the limed soil.

DIVERGENT EFFECTS OF LIMING THE TWO SOILS

Comparison of the results of applications of lime to the Dunkirk soil with those obtained from the Volusia soil shows some striking differences. It will be remembered that the Dunkirk soil contained about 50 per cent more calcium in the surface foot than does the Volusia soil, and that this ratio gradually increased with the depth, the fourth foot of the Dunkirk soil containing 319 per cent more than the corresponding layer of the Volusia. The lime requirement of the two soils by the Veitch method was about the same when averaged for the four feet, altho it was slightly greater in the surface foot of the Volusia. It is evident that the lime requirement as determined is not a measure of the calcium content of these soils.

In the light of this information it is interesting to observe the effect of liming in order to ascertain whether the calcium content or the lime requirement is the better guide to the need of the soils for lime as expressed by their response in crop yield. The records for the Dunkirk soil show that there was no larger yield on the limed tanks than on the unlimed. On the Volusia soil there was a consistently larger yield on the limed soil each

year except the first, and this increase averaged somewhat more than 12 per cent for the five-years period. The calcium content therefore appears to be a better guide to the need of these soils for lime than does the lime requirement as determined by the Veitch method. The data at hand are too limited to admit of generalization, but they may be worth further consideration.

Greater crop yield on the limed Volusia soil was accompanied by more nitrogen in the drainage water and also by more calcium. On the Dunkirk soil neither of these constituents was found in greater quantity in the drainage water from the limed tanks than from the unlimed. It may be remarked also that analyses of the soil air aspirated from the tanks, as reported in a previous publication,[4] showed no appreciable difference between the limed and the unlimed Dunkirk soil, but in the Volusia soil the carbon-dioxide content of the soil air was much increased by liming.

The fact that nitrate nitrogen in the drainage water and carbon dioxide in the soil air were present in larger amounts in the limed Volusia than in the unlimed gives evidence that decomposition of the organic matter proceeded more rapidly when lime was applied to that soil. This, however, was not the case with the Dunkirk soil, and there is presented the rather unlooked-for situation in which lime increased decomposition of organic matter in one soil but did not do so in the other soil.

A possible explanation for this divergent effect of lime on the two soils is suggested by the quantity of calcium in their respective drainage waters. As before stated, the application of lime had no effect on the removal of calcium in the drainage water from the Dunkirk soil, but it increased markedly the quantity of calcium removed from the Volusia soil. It seems probable that by increasing the concentration of calcium in the soil water, the ammonifying, nitrifying, and other bacteria concerned in decomposition of organic matter were afforded a more congenial environment. If liming did not increase the concentration of calcium in the soil water, as was the case with the Dunkirk soil, there was no acceleration of decomposition.

This experiment would seem to demonstrate one way in which liming may benefit soils. Certainly a larger amount of nitrate nitrogen was placed at the disposal of the plants, and the increased decomposition

[4] Bizzell, J. A., and Lyon, T. L. The effect of certain factors on the carbon-dioxide content of soil air. Amer. Soc. Agron. Journ. 10: 97–112. 1918.

doubtless rendered other plant nutrients more available by breaking down the compounds in which they were held, as, for instance, the phosphorus of organic matter.

SUMMARY

The object of the experiments here described was to observe the removal, by drainage water and by crops, of calcium and certain other soil constituents from Volusia silt loam. This soil is a rather unproductive type widely distributed over the hills of southern New York. The experiments continued thru a period of five years.

The average annual rainfall for the five years was 32.97 inches. Of the annual rainfall, 27.13 inches, or 82.3 per cent, percolated thru the unplanted soil, and 20.62 inches, or 62.5 per cent, percolated thru the cropped soil. About two-fifths of the rainfall passed into the air from the surface of the soil and thru the plants growing on it.

Application of burnt lime had no appreciable effect on the proportion of rainfall that percolated thru the soil. Similar experiments with Dunkirk soil reported elsewhere gave similar results. Liming either of these soils would probably not facilitate the removal of water thru tile drains.

The average evapo-transpiration ratio for the cropped soils was 1:908, the crops being maize, field peas, oats two years, and barley. The average minimum transpiration ratio for the same crops was 1:451. Both of these ratios were much wider for the Volusia soil of these experiments than for the Dunkirk soil in the experiments previously reported. In this comparison the soil having the greater production of dry matter in crops per unit of water used was the one that had the greater concentration of total solids in the drainage water.

The application of lime apparently favored the production of nitrates in the Volusia soil used in these experiments, while it had no such effect on the Dunkirk soil. The lime requirement of the Dunkirk soil as determined by the Veitch method is very little less than that of the Volusia. The percentage of calcium is about one-third less in the surface foot of the Volusia. In this case the relative calcium content of the soil is a better guide to the need of the soil for lime than is the lime requirement as determined.

The amount of nitrogen in the maize, allowing for that in the roots, added to that in the drainage water from the same tanks, was greater than the amount in the drainage water from the corresponding bare tanks; whil-

in the case of oats the amount of nitrogen in the crop and in the drainage water was less than in the drainage water from bare soil. The same relation held with the Dunkirk soil.

The quantity of calcium in the drainage water of the unplanted soil was greater than that in the crops and the drainage water combined from the cropped soil. Therefore the process of cropping conserves the calcium in the soil even when the crops are removed. This may be accounted for, in part at least, by the large formation and leaching of nitrates from bare soil.

Apparently the application of burnt lime to the Volusia soil increased the amount of soluble calcium in that soil, but this was not the case with the Dunkirk soil. The Volusia soil has a greater lime requirement and a lower calcium content than has the Dunkirk soil.

To keep the soil supply of calcium up to its present amount would require an annual application of 536 pounds of pure burnt lime, or 957 pounds of pure limestone, to supply the bare soil, and 371 pounds of burnt lime, or 662 pounds of limestone, to supply the planted soil.

Magnesium was present in the drainage water in much smaller quantity than was calcium. Application of lime to the soil increased the quantity of magnesium in the drainage water. Cropping decreased the removal of magnesium from the soil. These relations were the same as for the Dunkirk soil.

Potassium was removed in larger quantity in the drainage water than in the crops, in which respect the Volusia soil differed from the Dunkirk soil. It agreed with the latter, however, in that the application of lime did not increase the quantity of potassium in the drainage water nor in the crops.

Cropping did not materially affect the total removal of sulfur from the soil. Applications of lime resulted in a slight decrease in the sulfur removed in the drainage water. With the Dunkirk soil, applications of lime increased the amount of sulfur removed in the drainage water.

Phosphorus was present in the drainage water only in amounts too small to be determined. Applications of lime increased the removal of phosphorus in the crops. With the Dunkirk soil, applications of lime did not increase the removal of phosphorus in the crops.

Memoir 38, *The Crane-Flies of New York. Part II Biology and Phylogeny*, the third preceding number in this series of publications, was mailed on July 18, 1921.

Memoir 39, *The Genetic Relations of Plant Colors in Maize*, the second preceding number in this series of publications, was mailed on July 19, 1921.

APPENDIX

TABLE 1. CROP YIELDS FROM LYSIMETER TANKS 13 AND 15 DURING THE PERIOD FROM 1913 TO 1917, EXPRESSED AS DRY MATTER

Year	Tank	Crop	Per tank			Per acre		
			Grain (grams)	Cob (grams)	Straw, stover, or vines (grams)	Grain (bushels)	Cob (tons)	Straw, stover, or vines (tons
1913	13	Oats	364 2		302 3	62 4		0 83
	15	Oats	337 5		285 5	57 8		0 78
1914	13	Peas	95 6		452 2	8 8		1 24
	15	Peas	172 9		486 5	15 8		1 31
1915	13	Maize	31 2	22 5	716 3	3 0	0 06	2 05
	15	Maize	121 6	68 4	821 8	11 9	0 18	2 26
1916	13	Oats	184 8		266 7	31 6		0 72
	15	Oats	181 0		293 5	31 0		0 80
1917	13	Barley	148 4		161 2	17 0		0 44
	15	Barley	191 0		212 0	21 8		0 58

TABLE 2. FLOW OF DRAINAGE WATER FROM LYSIMETER TANKS 13 TO 16 FROM MAY 1, 1913, TO APRIL 30, 1918

(In liters)

Year and month	Tank			
	13	14	15	16
1913–May	56 8	71 2	70 4	72 0
June	2 4	24 0	3 2	23 [illegible]
July	0 0	5 6	0 8	1 8
August	0 4	0 8	0 0	0 0
September	17 6	72 0	0 8	67 2
October	37 6	124 0	26 4	92 0
November	91 6	115 2	79 2	89 6
December	49 2	54 0	44 8	41 6
1914–January	87 6	90 8	116 0	156 4
February	27 2	51 2	38 0	10 4
March	159 2	211 6	206 8	188 0
April	220 8	288 4	215 2	149 2
Totals	750 4	1,108 8	801 6	924 4

TABLE 2 (*continued*)

Year and month	Tank			
	13	14	15	16
1914 May	102 4	130 0	98 4	100 0
June	24 8	59 2	22 4	65 6
July	0 0	23 2	0 4	16 8
August	5 6	220 0	0 0	152 0
September	17 6	64 0	3 2	87 2
October	0 0	2 4	0 0	0 0
November	0 4	19 2	0 0	4 0
December	28 4	55 2	15 6	57 2
1915-January	221 6	278 0	246 8	285 2
February	224 0	179 2	339 6	304 0
March	5 2	2 4	12 0	3 2
April	5 6	1 6	3 2	1 6
Totals	635 6	1,034 4	741 6	1,076 8
1915 May	18 0	25 2	14 4	31 2
June	77 2	85 6	63 2	66 8
July	242 0	292 0	183 6	234 0
August	26 8	114 8	10 0	94 4
September	14 4	75 6	6 0	52 8
October	146 8	178 0	111 2	144 4
November	29 2	43 6	26 4	30 8
December	69 2	67 2	56 0	66 4
1916-January	90 4	86 4	72 8	73 6
February	4 8	8 0	6 4	5 2
March	96 8	143 6	109 6	137 6
April	238 8	268 4	187 6	178 4
Totals	1,054 4	1,388 4	847 2	1,115 6
1916 May to June 5	166 0	165 6	100 4	114 8
June 6				
July				
August	241 6	454 8	224 0	366 0
September				
October				
November				
December	76 8	72 8	85 2	65 6
1917 January 15				
January 16				
February				
March	162 4	142 8	130 0	132 8
April				
Totals	646 8	836 0	539 6	679.2

TABLE 2 (*concluded*)

Year and month	Tank			
	13	14	15	16
1917–May	178 8	194 8	171 6	172 4
June	282 0	345 6	228 0	330 0
July	46 8	80 8	39 6	83 2
August	268 4	296 4	214 0	318 4
September	48 8	62 4	57 6	61 6
October	203 2	219 6	186 0	216 0
November	24 0	20 0	22 4	17 2
December	15 2	17 6	24.8	21 8
1918–January	0 4	0 0	1 2	0 0
February	0 0	64 4	50 8	52 8
March	32 0	73 6	29 2	66 8
April	192 8	143 2	152 8	142 8
Totals	1,292 4	1,518 4	1,178 0	1,486 0
Grand totals	4,379 6	5,886 0	4,108 0	5,282 0

TABLE 3. FLOW OF DRAINAGE WATER FROM LYSIMETER TANKS 13 TO 16 FROM MAY 1, 1913, TO APRIL 30, 1918

(In acre inches)

Period	Tank			
	13	14	15	16
May 1, 1913, to April 30, 1914	18 23	26 94	19 48	22 46
May 1, 1914, to April 30, 1915	15 14	25 13	18 02	26 17
May 1, 1915, to April 30, 1916	25 62	33 74	20 59	27 11
May 1, 1916, to April 30, 1917	15 72	20 31	13 11	16 50
May 1, 1917, to April 30, 1918	31 40	36 90	28 62	36 11
Average annual percolation	21 28	28 60	19.96	25 07

TABLE 4. METEOROLOGICAL RECORDS AT ITHACA, MAY 1, 1913, TO APRIL 30, 1918
Data by months

Year and month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
1913-May	3.15	66.2	44 5	55 4	286 9	9 8	73
June	2 00	78.6	51 4	65 0	332 2	7 5	68
July	1.59	82.5	68.2	70 4	304 7	8 4	69
August	1 92	82 0	57 2	69 6	304 2	8 2	71
September	3 28	73 0	49 2	61 1	219 7	8 1	76
October	3 63	61 3	45 4	53 4	152 5	9 4	86
November	2 21	51 5	35 8	43 6	101 5	11 9	81
December	1 94	39 8	25 3	32 6	84 9	10 0	83
1914-January	1 37	33 7	19 3	26 5	56.7	13 8	85
February	1 62	27 0	8.5	17 8	151 4	11 6	82
March	1 90	39 1	24 3	31 7	141 7	10 3	82
April	4.35	51 1	33 1	42 1	144 8	11 6	78
May	3 63	71 1	47 5	59 3	297.7	8 1	71
June	4.75	76 5	54 5	65 5	301 2	8 5	74
July	1 89	81 2	59 2	70 2	230 8	7 0	78
August	6 10	80 2	58 2	69 2	208 4	7 0	80
September	1 96	71 1	48 2	59 6	255 2	7 6	82
October	1 38	63 6	43 9	53 8	212 5	8 7	86
November	0 68	46.4	31 1	38 8	111 9	12 5	78
December	2 70	32 9	19 1	26 0	73 3	10 1	82
1915-January	5 02	33 4	19 7	26 6	96 0	10 4	85
February	1 83	37 8	22 7	30.2	94 1	11 9	86
March	0 32	37 5	21 9	29.7	183 5	10 9	83
April	0 55	62 7	39 6	51 2	202 2	9 0	70
May	2 44	61 6	41 6	51 6	187.7	8 4	74
June	3 94	75 7	51 6	63 6	273.4	8 4	69
July	6 18	80 2	58 2	69 2	212 8	6 3	82
August	3 70	75 0	57 5	66 2	174 0	7 9	86
September	2 58	75 6	54 1	64 8	203.6	7.9	86
October	4 10	59 9	43 7	51 8	155 8	9 4	83
November	1 10	47 7	33 1	40 4	107.9	12 1	73
December	2 90	33 6	23 3	28 4	42 6	12 0	84
1916-January	0 81	40 0	23 7	31 8	73 7	12 2	80
February	2 97	30 1	13 0	21 6	87 8	10 1	83
March	2 28	35 3	18 7	27 0	162 5	10 9	81
April	2 77	53 7	37 0	45 4	133 4	8 4	80
May	4.27	68 4	46 9	57 6	180 2	10 6	71
June	3.48	70 9	51 9	61 4	171 0	9 8	79
July	1 29	85 8	63 5	74 6	226 7	7 8	77
August	1 50	83 7	58 7	71 2	283 2	7 3	75
September	5 65	72 8	50 9	61 8	232 7	9 5	73
October	1 59	63 1	39 6	51 4	180 5	9 7	74
November	1 53	46 7	31 4	39 0	88 5	10.2	77
December	1.01	35.9	22.0	29.0	99.9	12.1	79

TABLE 4 (*continued*)

Year and month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m (per cent)
		Mean maximum	Mean minimum	Mean			
1917–January	1 82	34 1	17 7	25 9	101 8	12.9	84
February	0 70	29 6	10 4	20 0	99 1	13 5	86
March	1 59	41 9	25 9	33 9	127 1	14 2	78
April	1 83	52 4	35 5	44 0	140 9	10 9	75
May	4 41	56 7	40 0	48 4	107 9	10.6	72
June	7 35	74 1	53 6	63 8	167 8	8.0	76
July	3 25	81 4	61 6	71 5	250 8	7 5	76
August	8 45	79 9	58 5	69 2	244 8	7 5	80
September	2 22	69 9	47 2	58 6	231 2	7 6	82
October	4 84	53 6	36 7	45 2	77 8	10 8	81
November	0 64	43 3	26 4	34 8	93 6	9 6	81
December	2 48	26 9	10 7	18 8	72 2	12 1	82
1918–January	1 83	22 0	6 8	14 4	127 0	10 9	79
February	1 48	35 0	13 7	24 4	104 8	14 6	77
March	2 58	48 2	25 3	36 8	178 6	11 3	73
April	3 54	56 3	35 2	45 8	171 2	10 3	75

Average of each month

Month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m (per cent)
		Mean maximum	Mean minimum	Mean			
May	3 58	64 8	44 1	54 5	213.9	9 5	72 2
June	4 30	75 2	52 6	63 9	249 1	8 4	73 2
July	2 84	82 2	62 1	71 2	245 2	7 4	76 4
August	4 33	80 2	58 0	69 1	242 9	7 6	78 4
September	3 14	72 5	49 9	61 2	228 5	8 1	79 8
October	3 11	60 3	41 9	51 1	155 8	9 6	82 0
November	1 23	47 1	31 6	39 3	100 7	11 3	79 0
December	2 21	33 8	20 1	26 96	74 6	11 3	82 0
January	2 17	32 6	17 4	25 0	91 0	12 0	82 6
February	1 72	31 9	13 7	22 8	107 4	12 3	82 8
March	1 73	40 4	23 2	31 8	158 7	11 5	79 4
April	2 60	55 2	36 1	45 7	158 5	10 0	75 6

TABLE 4 (*concluded*)
Data by years

Year	Total rainfall (inches)	Temperature (degrees Fahrenheit)			Total hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
May 1913, to April 1914	28 96	57 2	38 5	47 4	2,281.2	10.1	77 8
May 1914, to April 1915	30 81	57 9	38 8	48 3	2,266 8	9 3	79 6
May 1915, to April 1916	35 77	55 7	37 9	46 8	1,815.2	9 5	80 5
May 1916, to April 1917	26 26	57 1	37 9	47 5	1,940 6	10 7	77 3
May 1917, to April 1918	43 07	53 9	34 6	44 3	1,827 7	10 1	77 8

TABLE 5. SUBSTANCES CONTAINED IN DRAINAGE WATER, IN PARTS PER MILLION

	Tank			
	13	14	15	16
	TOTAL SOLIDS			
1913–14				
May 1–September 30	246	314	237	422
October 1–April 30	177	220	199	310
1914–15				
May 1–September 30	241	245	223	370
October 1–April 30	200	179	184	252
1915–16				
May 1–September 30	302	271	309	363
October 1–April 30	260	228	263	292
1916–17				
May 1–April 30	296	270	325	353
1917–18				
May 1–April 30	285	369	295	306
Averages	251	262	254	333.5
	NITRATES			
1913–14				
May 1–September 30	40 0	66 0	42 0	116 0
October 1–April 30	8 7	50 8	19 2	68.3
1914–15				
May 1–September 30	6 0	30 7	14 6	55 4
October 1–April 30	7 6	22.9	22.2	42 2
1915–16				
May 1–September 30	20 6	42 0	25 3	57 3
October 1–April 30	8 0	18 5	7 8	27 3
1916–17				
May 1–April 30	6 5	36 0	5 8	60 0
1917–18				
May 1–April 30	3 0	20 5	3 0	25 0
Averages	12 56	35 93	17 48	56 44

TABLE 5 (*continued*)

	Tank			
	13	14	15	16
	BICARBONATES			
1913–14				
May 1–September 30	170	197	169	213
October 1–April 30	142.3	126.8	153.8	146.8
1914–15				
May 1–September 30	170	163	168.75	207
October 1–April 30	161 1	131.5	127 3	135
1915–16				
May 1–September 30	200	171.5	226 5	251
October 1–April 30	212 5	153	201 5	206 5
1916–17				
May 1–April 30	244 3	194.5	288.8	246 8
1917–18				
May 1–April 30	255	217	280	234
Averages	194 4	169.29	201 96	205 01
	SULFATES			
1913–14				
May 1–September 30	23	33	39	57
October 1–April 30	22 8	15.9	18.3	15 5
1914–15				
May 1–September 30	10 6	7.1	13.9	8 0
October 1–April 30	17 2	23.4	12.2	14 3
1915–16				
May 1–September 30	36 0	22.6	22 4	22 9
October 1–April 30	34 8	26.3	33 0	23 0
1916–17				
May 1–April 30	34 5	27.0	34 5	27 0
1917–18				
May 1–April 30	21 5	16.3	19 1	19 2
Averages	25 05	21 46	24 09	23 36
	SILICA			
1913–14				
May 1–September 30	5 6	6 3	5.8	6 8
October 1–April 30	7.1	5.9	8.4	8 9
1914–15				
May 1–September 30	6.6	9.4	5.4	12 0
October 1–April 30	6.6	4.5	5.5	5 4
1915–16				
May 1–September 30	8 9	8.0	8.6	10 5
October 1–April 30	5 5	4.9	7.6	5 5
1916–17				
May 1–April 30	9 0	8.7	10.3	7 6
1917–18				
May 1–April 30	11 8	11 4	10 3	10 2
Averages	7 64	7 39	7 74	8 36

TABLE 5 (*continued*)

	Tank			
	13	14	15	16
	PHOSPHATES			
1913–14				
May 1 September 30	None	None	None	None
October 1 April 30				
1914–15				
May 1 September 30	Trace	Trace	None	Trace
October 1–April 30	Trace	Trace	Trace	Trace
1915–16				
May 1 September 30	None	None	None	None
October 1 April 30	None	None	None	None
1916–17				
May 1 April 30	Trace	Trace	Trace	Trace
1917–18				
May 1–April 30	None	None	None	None
	CALCIUM			
1913–14				
May 1 September 30	38 5	56 3	40.9	70 8
October 1–April 30	42 2	49.8	49.7	62.4
1914–15				
May 1–September 30	46 1	49.0	47.5	77.2
October 1 April 30	65 3	37.8	43.8	52.8
1915–16				
May 1 September 30	52 8	50.8	64.7	71 0
October 1 April 30	49 3	41.0	50.1	62.1
1916–17				
May 1–April 30	58 1	52.9	71.7	77 5
1917–18				
May 1 April 30	56 6	54 2	63 1	64 4
Averages	51 12	48 99	53 95	67 28
	MAGNESIUM			
1913–14				
May 1 September 30	5 8	7.6	6.8	9.0
October 1 April 30	6 3	6.7	6.9	9 4
1914–15				
May 1 September 30	5.6	6.0	6.0	9.2
October 1 April 30	4 5	4.2	8.6	5.4
1915–16				
May 1 September 30	7 8	7.6	7.9	3.6
October 1 April 30	6.7	5.1	8.3	8.1
1916–17				
May 1 April 30	6 6	8 5	9.6	11.0
1917–18				
May 1 April 30	5 8	6.1	7.1	7.9
Averages	6 15	6.48	7.04	9.22

TABLE 5 (*concluded*)

	Tank			
	13	14	15	16
	POTASSIUM			
1913–14				
May 1–September 30	12 4	9 5	11 3	13 8
October 1–April 30	8 3	8 3	6.1	7 1
1914–15				
May 1–September 30	16 1	16 9	11.5	12 2
October 1–April 30	8 9	8 6	5 0	6 0
1915–16				
May 1–September 30	29 7	21 6	20 7	17 2
October 1–April 30	18 9	13 8	14 3	9 9
1916–17				
May 1–April 30	22 6	18 7	17.4	14 4
1917–18				
May 1–April 30	22 2	18 6	16 7	15 1
Averages	17 40	14 71	12 87	11 96
	SODIUM			
1913–14				
May 1–September 30	15 6	12 9	11 3	10 2
October 1–April 30	22 9	22 5	24 0	22 6
1914–15				
May 1–September 30	17 5	13 9	12 7	10 7
October 1–April 30	22 9	17 9	17 8	15 2
1915–16				
May 1–September 30	24 5	19 8	19 9	20 7
October 1–April 30	26 0	18 9	24.9	18 9
1916–17				
May 1–April 30	18 4	13 7	18 5	13 6
1917–18				
May 1–April 30	18 7	14 4	16 9	13 7
Averages	20 83	16 77	18 25	15 45
	CARBONATES			
1913–14				
May 1–September 30	None	None	None	None
October 1–April 30	None	None	None	None
1914–15				
May 1–September 30	3 68	Trace	Trace	4 92
October 1–April 30	None	None	None	None
1915–16				
May 1–September 30	7 62	6 40	None	7 37
October 1–April 30	7.84	4 41	9 31	4 90
1916–17				
May 1–April 30	None	None	None	None
1917–18				
May 1–April 30	None	None	None	None
Averages	2 39	1 35	1 16	2 15

TABLE 6. SUBSTANCES CONTAINED IN DRAINAGE WATER, IN POUNDS PER ACRE

	Tank			
	13	14	15	16
	TOTAL SOLIDS			
1913–14				
May 1–September 30	104 1	299 2	97 6	387 9
October 1–April 30	656 7	1,133 9	796 7	1,293 7
Totals	760 8	1,433 1	894 3	1,681 6
1914–15				
May 1–September 30	198 9	669 4	152 0	857 9
October 1–April 30	534 4	530 6	625 4	909 1
Totals	733 3	1,200 0	777.4	1,767 0
1915–16				
May 1–September 30	629 6	885 7	471 9	958 4
October 1–April 30	968 4	999 0	826 0	1,023 9
Totals	1,598 0	1,884 7	1,297 9	1,982.3
1916–17				
May 1–April 30	1,054 9	1,243 7	966 2	1,322.6
1917–18				
May 1–April 30	2,028 0	1,986 5	1,914 6	2,505.3
Yearly averages	1,235 0	1,549 6	1,170 1	1,851 7
	NITRATES			
1913–14				
May 1–September 30	16 5	62 8	17 1	106 3
October 1–April 30	32 4	261 8	76 8	285 1
Totals	48 9	324 6	93 9	391.4
1914–15				
May 1–September 30	4 9	83 7	9 9	128 4
October 1–April 30	20 4	67 7	75 5	90 9
Totals	25 3	151 4	85 4	219 3
1915–16				
May 1–September 30	42 9	137 2	38 6	151.2
October 1–April 30	29 8	81 0	24.5	95 7
Totals	72 7	218 2	63 1	246 9
1916–17				
May 1–April 30	23 1	165 8	17.2	224 8
1917–18				
May 1–April 30	20 9	171 3	19 3	204.4
Yearly averages	38.2	206 2	55 8	257 3

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	BICARBONATES			
1913–14				
May 1–September 30	71 6	187 3	69 4	195 6
October 1–April 30	527 9	653 5	615.7	612 6
Totals	599 5	840 8	685 1	808 2
1914–15				
May 1–September 30	140 5	445 2	115 1	479 9
October 1–April 30	430 3	389 5	432 5	487 1
Totals	570 8	834 7	547 6	967 0
1915–16				
May 1–September 30	417 0	560 5	345 9	662 7
October 1–April 30	791 5	670 3	632 8	724 1
Totals	1,208 5	1,230 8	978 7	1,386 8
1916–17				
May 1–April 30	870 6	895 9	858 6	924 7
1917–18				
May 1–April 30	1,814 9	1,814 9	1,817 2	1,915 9
Yearly averages	1,012 8	1,123 4	977 4	1,200 5
	SULFATES			
1913–14				
May 1–September 30	9 3	31 4	15 9	52 3
October 1–April 30	84 6	81 9	73 2	64 7
Totals	93 9	113 3	89 1	117 0
1914–15				
May 1–September 30	8 8	19 2	9 3	18 1
October 1–April 30	45 7	68 8	41 3	51 2
Totals	54 5	88 0	50 6	69 3
1915–16				
May 1–September 30	75 0	73 8	34 2	60 4
October 1–April 30	129 6	115 2	103 6	80 9
Totals	204 6	189 0	137 8	141 0
1916–17				
May 1–April 30	122 9	123 3	102 5	101 1
1917–18				
May 1–April 30	152 6	136 1	125 6	157 0
Yearly averages	125 7	129 9	101 1	117 1

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	SILICA			
1913–14				
May 1–September 30	2 2	6 0	2.2	6 0
October 1–April 30	26 3	30 4	33 6	37 1
Totals	28.5	36 4	35 8	43.1
1914–15				
May 1–September 30	5 5	25.3	3.3	27 5
October 1–April 30	17.6	13 2	18 7	19 3
Totals	23.1	38.5	22.0	46 8
1915–16				
May 1–September 30	18 5	26 1	13 1	27 7
October 1–April 30	20 5	21 4	23 8	19 3
Totals	39.0	47.5	36 9	47.0
1916–17				
May 1–April 30	32.0	40 3	31.8	24 4
1917–18				
May 1–April 30	83.7	95 3	66.6	83 2
Yearly averages	41 2	51 6	38 6	48 9
	CALCIUM			
1913–14				
May 1–September 30	15 9	53 4	16 5	65 0
October 1–April 30	156 4	256 8	198 9	260 4
Totals	172 3	310 2	215 4	325 4
1914–15				
May 1–September 30	38 0	133 9	32 5	179 0
October 1–April 30	174 1	111 8	148 7	190 6
Totals	212 1	245.7	181 2	369 6
1915–16				
May 1–September 30	110.0	165 0	98 9	187.6
October 1–April 30	183 8	179 8	157.5	217.7
Totals	293.8	344 8	256 4	405.3
1916–17				
May 1–April 30	207 0	243 6	213 1	290.3
1917–18				
May 1–April 30	402 8	452 9	409 4	526 7
Yearly averages	257 6	319 4	255 1	383 4

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	MAGNESIUM			
1913–14				
May 1–September 30	2.2	7 1	2.7	8 2
October 1–April 30	23 4	34 5	27.6	39 4
Totals	25.6	41 6	30.3	47 6
1914–15				
May 1–September 30	4 4	15 9	3 8	20 9
October 1–April 30	12.1	12 1	12 1	19 3
Totals	16 5	28 0	15 9	40 2
1915–16				
May 1–September 30	16 3	25 0	12 1	36 0
October 1–April 30	24.9	22 3	26 0	28 5
Totals	41 2	47 3	38 1	64 5
1916–17				
May 1–April 30	23.5	39 1	28 5	41 2
1917–18				
May 1–April 30	41 3	50 7	45 7	64 4
Yearly averages	29 6	41 3	31 7	51 6
	POTASSIUM			
1913–14				
May 1–September 30	4 9	8 8	4 4	12 6
October 1–April 30	30 9	42 8	24 2	29 8
Totals	35.8	51 6	28.6	42 4
1914–15				
May 1–September 30	13 2	46 3	7 7	8 1
October 1–April 30	23 1	25 3	16 5	21 5
Totals	36 3	71 6	24 2	29 6
1915–16				
May 1–September 30	61.9	70 7	31 6	45 4
October 1–April 30	70 5	60 4	44 9	34 7
Totals	132 4	131 1	76 5	80 1
1916–17				
May 1–April 30	80 5	86 1	51.7	53 9
1917–18				
May 1–April 30	158 1	155 4	108 0	123 4
Yearly averages	88 6	99 1	57 8	69.9

TABLE 6 (*concluded*)

	Tank			
	13	14	15	16
	SODIUM			
1913–14				
May 1-September 30	6 6	12.1	4 4	9.3
October 1-April 30	85 1	116 1	95 9	94 4
Totals	91.7	128.2	100.3	103 7
1914–15				
May 1 September 30	14 3	38 0	8 2	15 4
October 1-April 30	61 1	52 9	60 6	54 5
Totals	75 4	90 9	68 8	69 9
1915–16				
May 1-September 30	51 2	64 8	30 4	46 6
October 1-April 30	96 8	83 0	78 2	66.2
Totals	148 0	147 8	108 6	112 8
1916–17				
May 1-April 30	65 5	63 1	55 0	50 9
1917–18				
May 1 April 30	132 8	120 1	109 6	111 8
Yearly averages	102 7	110 0	88 4	89 8

TABLE 7. ASH AND ASH CONSTITUENTS IN CROPS, BY YEARS
(In percentage of dry matter)

Year	Tank	Crop	Part of crop	Ash	Ca	Mg	K	S	P
1913	13	Oats	Grain	3 67	0 03	0 06	0 62	0.24	0 56
	13	Oats	Straw	6 92	0 43	0 12	2.40	0.18	0 12
	15	Oats	Grain	3.39	0 04	0.03	0.62	0.23	0 56
	15	Oats	Straw	6 61	0.42	0 17	2 16	0 23	0 11
1914	13	Peas	Grain	4.30	0 05	0 04	1.15	0 36	0 48
	13	Peas	Straw	27 43	0 67	0 23	0 46	0 62	0 33
	15	Peas	Grain	3.43	0 04	0 04	1 14	0.33	0 48
	15	Peas	Straw	14 20	0.99	0.18	0 04	0 60	0 35
1915	13	Maize	Grain	1 74	0 03	0 09	0 38	0 30	0 36
	13	Maize	Straw	6 54	0 15	0 08	1 19	0.30	0 22
	15	Maize	Grain	1.60	0 06	0 07	0 42	0 18	0 37
	15	Maize	Straw	5 19	0 13	0 11	0 83	0 31	0 22
1916	13	Oats	Grain	3 33	0.02	0.03	0 77	0 19	0 47
	13	Oats	Straw	8 16	0.28	0 12	2 49	0 30	0 19
	15	Oats	Grain	3 88	0 01	0 04	0 67	0.18	0 52
	15	Oats	Straw	7 89	0 32	0.20	2 19	0.30	0 24
1917	13	Barley	Grain	3 01	0 03	0 02	0 54	0.21	0 52
	13	Barley	Straw	7 41	0 24	0 07	1.03	0.24	0 20
	15	Barley	Grain	2 92	0 02	0 03	0 58	0.20	0 50
	15	Barley	Straw	6 13	0 33	0 04	0 93	0.24	0 24

TABLE 8. ASH AND ASH CONSTITUENTS IN CROPS, BY YEARS
(In pounds per acre)

Year	Tank	Crop	Part of crop	Ash	Ca	Mg	K	S	P
1913	13	Oats	Grain	70 8	0 5	1 1	11 9	4 6	10 9
	13	Oats	Straw	116 9	7.3	2 0	40 5	3 1	2 0
	13	Oats	Total	187 7	7 8	3 1	52.4	7 7	12 9
	15	Oats	Grain	62 7	0 8	0 6	11 3	4 2	10 3
	15	Oats	Straw	103 2	6 1	2 6	33 7	3 5	1 7
	15	Oats	Total	165 9	6 9	3 2	45.0	7.7	12 0
1914	13	Peas	Grain	21 5	0 3	0 2	5 8	1.9	2 4
	13	Peas	Straw	679 5	16 5	5.7	11 3	5.5	8 2
	13	Peas	Total	701 0	16 8	5 9	17 1	17 4	10 6
	15	Peas	Grain	31 6	0 4	0 4	10 4	3 0	4 4
	15	Peas	Straw	391 2	27 4	4 9	11 4	16 6	9 6
	15	Peas	Total	422 8	27 8	5 3	21 8	19 6	14 0
1915	13	Maize	Grain	2 9	0 1	0 2	0 7	0 6	0 6
	13	Maize	Straw	264 8	6 0	3 2	47 9	12 0	9 0
	13	Maize	Total	267 7	6 1	3 4	48 6	12 6	9 6
	15	Maize	Grain	10 6	0 5	0 4	2 8	1 2	2 5
	15	Maize	Straw	231 7	5 7	4 9	37 2	13 6	9 9
	15	Maize	Total	242 3	6 2	5 3	40 0	14 8	12 4
1916	13	Oats	Grain	33 7	0 2	0 3	7 8	2 0	4 8
	13	Oats	Straw	118 1	4 1	1 8	36 1	4 3	2 8
	13	Oats	Total	151 8	4 3	2 1	43 9	6 3	7 6
	15	Oats	Grain	38 5	0 1	0 4	6 7	1 8	5 2
	15	Oats	Straw	126 1	5 3	3 3	35 1	4 8	3 8
	15	Oats	Total	164 6	5 4	3 7	41 8	6 6	9 0
1917	13	Barley	Grain	24 7	0 2	0 2	4 4	1 8	4 3
	13	Barley	Straw	65 6	2 2	0 7	9 1	2 1	1 8
	13	Barley	Total	90 3	2 4	0 9	13 5	3 9	6 1
	15	Barley	Grain	30 7	0 2	0 3	6 1	2 1	5 3
	15	Barley	Straw	72 9	3 9	1 7	11 0	2 9	2 9
	15	Barley	Total	103 6	4 1	2 0	17 1	5 0	8 2

JULY, 1921 MEMOIR 42

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

BEAN ANTHRACNOSE

MORTIER F. BARRUS

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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BEAN ANTHRACNOSE

BEAN ANTHRACNOSE

MORTIER F. BARRUS

THE HOST

Next to the potato and the sweet potato, the bean (considered as a vegetable) is the most important crop grown in this country. Not only are beans grown in practically every home garden, but they are of great commercial importance also. The United States Census Bureau (1913a) reports the production of dry edible beans grown for commercial purposes in this country during 1909 as 11,251,160 bushels, or more than double that of 1899, representing a value of $21,771,482. The Monthly Crop Report of the United States Department of Agriculture (1917: 133) estimates the production for 1916 as 12,029,000 bushels; for 1917 it was 18,129,000 bushels, the culture of beans having been stimulated by the demand and by the high prices paid as a result of the war. Since the war there has been a marked reduction in area in the States having a high bean production. Dry beans are a staple crop in New York, Michigan, Colorado, New Mexico, California, and several other States, while string beans are grown extensively in many parts of the country as a truck crop. In northern New York, in Michigan, Colorado, and California, and in southern Canada, the production of garden and field beans for seed has developed into a large and profitable industry. Large areas also are devoted to the production of snap beans for canning.

Prior to 1899, New York was the leading State in the production of dry edible beans, in 1879 producing 42.4 per cent of the total crop in the United States and in 1889 producing 35.1 per cent. In 1909, however, it produced only about 15 per cent of the total crop (U. S. Census Bureau, 1913a). While production has greatly increased in the other large bean-producing States (table 1), New York has lagged behind, although it was stirred on somewhat during 1917 and 1918.[1] Low yields resulting from disease and from poor weather conditions inevitably resulted in reduced acreage for 1919.

[1] Data for 1879 and 1889 were obtained from the Eleventh Census; for 1899 and 1909, from the Thirteenth Census; for 1914, from the Monthly Crop Report for 1916, for 1915, 1916, and 1917, from the Monthly Crop Report for 1917; for 1918, from the Monthly Crop Report for 1918; for 1919, from the Monthly Crop Reporter for 1919, for 1920, from the Monthly Crop Reporter for 1920. These references are given under *Literature Cited*, page 199.

TABLE 1. ACREAGE AND PRODUCTION (IN BUSHELS) SINCE 1879, OF DRY EDIBLE BEANS IN THE FIVE LARGEST BEAN-PRODUCING STATES AND IN THE UNITED STATES

Year		New York	Michigan	California	Colorado	New Mexico	United States
1879	Production	1,303,444	167,658	378,971	.	16,168	3,075,050
1889	Production	1,111,510	434,014	713,480	7,265	7,843	3,163,554
1899	Acreage	129,298	167,025	45,461	2,406	17,417	453,841
	Production	1,360,445	1,806,413	658,515	28,570	36,022	5,064,490
1909	Acreage	115,698	403,669	157,987	5,040	20,766	802,991
	Production	1,681,506	5,282,511	3,328,218	53,926	85,795	11,251,160
1914	Acreage	118,000	490,000	215,000	20,000	32,000	...
	Production	1,650,000	5,488,000	3,875,000	300,000	272,000	. .
1915	Acreage	130,000	506,000	225,000	21,000	46,000	.....
	Production	1,495,000	4,250,000	3,868,000	340,000	368,000	.
1916	Acreage	190,000	470,000	340,000	38,000	64,000	1,244,000
	Production	1,140,000	3,102,000	5,576,000	424,000	425,000	12,029,000
1917	Acreage	210,000	639,000	558,000	193,000	213,000	2,117,29
	Production	1,575,000	3,514,000	8,035,000	1,467,000	958,000	18,129,000
1918	Acreage	200,000	543,000	592,000	252,000	149,000	
	Production	1,600,000	4,887,000	8,880,000	1,638,000	596,000	
1919	Acreage	90,000	300,000	400,000	69,000	123,000	
	Production	1,305,000	4,140,000	5,000,000	448,000	922,000	
1920	Acreage	90,000	275,000	285,000	63,000	121,000	
	Production	1,260,000	3,575,000	2,850,000	504,000	811,000	

The figures in table 2, taken from statistics compiled by order of the New York State Food Commission (1919), give the acreage and production during 1917 of important bean-growing counties in the State and show the location of the bean area. A larger yield to the acre was obtained by some of the other counties which planted a smaller acreage.

TABLE 2. ACREAGE AND PRODUCTION OF FIELD BEANS IN THE TEN LARGEST-PRODUCING COUNTIES OF NEW YORK STATE IN 1917

County	Acreage	Production (bushels)
Livingston	37,010	325,245
Wyoming	23,146	200,949
Genesee	18,835	101,158
Ontario	13,884	82,353
Wayne	12,615	86,105
Monroe	11,076	42,751
Orleans	9,640	38,561
Erie	9,235	46,547
Yates	9,007	70,442
Schuyler	8,164	59,650
New York State	218,742	1,477,061

New York ranks first of all the States in the amount and value of canned ring beans, the United States Census Bureau (1913b) reporting 452,634 ses having a value of $839,135, or more than half the total value or the entire country. It is assumed that nearly all string beans canned n the States were grown within its territory.

It is thus seen that the bean industry in New York and in the country t large is an important one, and well worthy any attention that may be iven to it by the Federal Government and by the various experiment tations.

The common bean (*Phaseolus vulgaris* L.) becomes affected at times y various diseases, among which the bean anthracnose is an important ne in New York State. Bacterial blight also occurs frequently on the ommon bean and on the lima bean (*P. lunatus* L.), and was severe in 916 and 1917. Root rots — especially the one caused by *Fusarium Iarti phaseoli*, though black root rot, caused by *Thielavia basicola* Zopf., ould be mentioned also — are causing considerable loss in restricted calities and may be more prevalent than is generally known. Rhizoctonia tem canker and pod spot, caused by *Corticium vagum* B. & C., has been eported from a few places as being serious and is known to have a general istribution. Bean rust, caused by *Uromyces appendiculatus* (Pers.) év., occurs occasionally, but does little damage in this State though it severe at times in the South and the West. Brown rot, caused by *clerotinia libertiana* Fuckel, is destructive only during periods of extended ains and warm weather, and then only on vines so bushy that they do ot permit good aëration. The leaf spot caused by *Phyllosticta* sp. is ncommon in the State, while leaf spot caused by *Isariopsis griseola* acc. has not been reported here.

In addition to the parasitic diseases just mentioned, mosaic, supposed o be due to a filterable virus, should certainly be included because of its eneral prevalence in the State and its apparently serious effect.

The writer has devoted more or less of his time for the past ten years o the study of the anthracnose disease and the manner of its control. n the following pages he presents his opinions and those of others in gard to the disease, and records the results of his experiments.

THE DISEASE

ECONOMIC ASPECTS

Name, history, and geographical distribution

The name *bean anthracnose*, generally applied by American, English, French, Italian, and other pathologists to the disease under consideration, was apparently first used in this connection by Scribner (1888), although the name *anthracnose* was used earlier to designate the grape disease caused by *Gloeosporium ampelophagum* Sacc. The terms *pod spot*, or *canker*, and *leaf spot* are sometimes applied to the disease as it occurs on these respective parts of the plant; while not uncommonly the terms *rust* and *blight*, and rarely *scab*, are erroneously used by laymen. Frank (1883 b) called the disease *Fleckenkrankheit*, and the names *Brennerflecken*, *Brennerfleckenkrankheit*, *Brennfleckenkrankheit*, and *Schwarzfleckenkrankheit* have been used by German writers. In Holland, Schenk (1917) speaks of the disease as *Vlekziekte*, and in Denmark it is called *Bonnesyge* by Lind (1910).

The disease was first definitely described by Saccardo (1878), who reported its discovery by Lindemuth in the fruit and vegetable garden of the Agricultural Institute of Poppelsdorf, at Bonn, in August, 1875. Anthracnose spots are present, however, on specimens of bean pods distributed by Desmazières (1843 b) under the name *Septoria leguminum* Nob. Berkeley (1880) reports the disease on kidney beans from Bedford, England, ascribing it to Ascochyta. Saccardo (1881) shows a good colored reproduction of a pod affected with anthracnose, and drawings of the fructifications of the fungus. The label indicates that the fungus was collected at Padua in June, 1875, on *Phaseolus vulgaris*. Frank (1883 b) states that Lindemuth reported to him the occurrence of the disease in 1875 on the red-mottled Zucker-Stangenbrechbohnen, and a few years later on numerous other varieties grown in the same vicinity. Frank himself says the disease occurred in other parts of Germany in 1881 and in various localities in 1882, it being especially severe the latter year. He gives an excellent account of the disease and its cause in the article cited. Saccardo (1884) mentions the disease as being common and injurious in Germany, Italy, France, England, and North America. Richon (1889) records its presence in the Marne district of France.

Ellis and Everhart (1885:111) report Dr. Farlow's observations of the common occurrence of this fungus on beans in the Cambridge (Massachusetts) market since 1882. From the Plant Disease Bulletin issued by the Plant Disease Survey of the United States Plant Industry Bureau (1918.254), it appears that the disease was reported from Pennsylvania, Maryland, and Louisiana in 1887; from Michigan in 1889; and from New York and Ohio in 1890. Scribner (1888:361), after speaking of its distribution in Europe, says that specimens have been received from Maine, Massachusetts, Wisconsin, Pennsylvania, Louisiana, and the District of Columbia.

Since then the disease has been reported from a number of places in Germany, Italy, England, and the United States. Reports of its existence — some recording only its presence and others its prevalence and destructiveness — have been recorded from Norway (Schoyen, 1901), Sweden (Eriksson, 1889), Denmark (Lind, 1910), Russia (Jaczewski, 1912), Tyrol (Bubák and Kabát, 1904), Belgium (Marchal, 1907), Holland (Sprenger, 1918), Ireland (Schoebotham, 1909), Japan (Ideta, 1911), Formosa (Fujikuro, 1914), India (Butler, 1918), Transvaal (Pole-Evans, 1907), Australia (Cooke, 1892), New Zealand (Kirk, 1905), Argentina (Spegazzini, 1899), Brazil (Puttemans, 1901), Cuba (Cook and Horne, 1908), Alaska (Anderson, 1916), and Canada (Craig, 1893).

From the bulletin issued by the Plant Disease Survey (U. S. Plant Industry Bureau, 1918) and from the earlier survey reports by Orton and by Orton and Ames (1904–1909), as well as from the bulletins and reports of the various experiment stations in this country, it appears that the disease has occurred at one time or another in every State in the Union except South Dakota, Wyoming, and Nevada. Doubtless it has occurred in these three States also but has not been reported.

It is thus seen that the disease is world-wide in its distribution, occurring in nearly every place where beans are grown. The climatic condition of a country or a region has much to do with the development of the disease, so that in some of the countries where it has been reported it is of no importance and in others it becomes a serious pest. While it has been reported from Alaska, it cannot be enphytotic there, as seed of *Phaseolus vulgaris* will not mature in that latitude; but the summer climate of Alaska is not unfavorable for the development of the fungus when introduced in imported seed affected by it.

Economic importance

While bean anthracnose can be found on some plants year after year, it is only during certain periods most favorable for its development that it becomes widespread and causes serious loss. Such epiphytotics are coincident with or closely follow periods of rather abundant rainfall during the growing season, and often recur in three or more successive years. Frank (1883b:512), as already noted, reports such an epiphytotic in Germany in 1882. Querner (1908) reports one in 1908, and Fischer (1919:246) reports epiphytotics in 1915 and 1916. Voglino (1892) reports a complete destruction of the crop in 1891 in several localities in Italy.

Beach (1892:308) reports a heavy loss in many sections of New York in 1891. Halsted (1893–1901) reports the disease as common from 1892 to 1897, after which it was an unimportant factor in his experiments. Whetzel (1908:436) reports the disease as widespread in New York in 1906. Then followed five years during which the loss in most sections of the State was negligible. Late in the season of 1911, the disease was observed or reported from many fields, and in 1912 it was again severe. The following year there was very little anthracnose to be found except in restricted areas, but it was present to a destructive degree in 1914 and 1915, the loss during the latter year ranging from 30 to 100 per cent of the crop except in a few cases where resistant varieties were grown. During 1916 the damage done in this State was slight, but the disease appeared again from 1917 to 1919, the losses in these years, however, being much less than in earlier years.

A study of the table given in the Plant Disease Survey bulletin (page 254 of the reference already cited) shows that bean anthracnose was generally severe in the eastern United States from 1906 to 1908, from 1914 to 1915, and again in 1917. Individual reports of its severity are recorded in other years. In Maine and New Hampshire it is reported as causing considerable loss nearly every year, while in Western States it rarely does any damage although it may be present.

Figures are not obtainable to show the exact loss from this disease, but in epiphytotic years it is very large, amounting in individual cases to 100 per cent. Muncie (1917:7) estimates a loss in Michigan of $1,500,000 in 1914 and of about $3,000,000 in 1915, while the loss in New York in 1915 probably amounted to $700,000 or more. The Plant Disease Survey

bulletin (page 13 of reference cited) gives the loss during 1917 for New York as 5 per cent, or 83,000 bushels, and for the United States as 1.76 per cent, or 363,000 bushels.

The losses from bean anthracnose are due to poor germination of affected seed, to destruction of affected seedlings, to low yield of affected plants, and to decreased value of the product. The principal loss in the production of green beans is due to the spotting of the pods, which renders them unsalable as snap beans and unfit for canning. Southern-grown beans, apparently healthy when shipped, frequently reach northern markets in a badly spotted condition, and if the disease is common in the field, pods kept over night after picking are likely to be rusted the next morning. The lesion may extend through the pod to the seed, discoloring it. The value of dry seed thus affected is lessened, and the buyer usually deducts a certain percentage, the "pick," from the total weight to allow for this depreciation. A poor stand often results from the planting of spotted seeds, many of which fail to germinate, and this result is augmented by the destruction of seedlings subsequently affected. Plants that have survived the early attack may give an inferior yield due to interrupted growth, although the pods themselves may not become spotted.

SYMPTOMATIC ASPECTS

While the appearance of anthracnose on the various parts of the bean plant has been described accurately by several investigators, a description is included here of its appearance as observed on different varieties of beans under different conditions and at different stages of maturity.

On the seed

The seed of the bean may be discolored by anthracnose, blight, rhizoctoniose, and brown rot, and by various mold-producing fungi. The appearance most characteristic of anthracnose (Plate IV) is the decided blackening of the affected parts. Usually the blackened area has a tawny brown or tan-colored[2] border, or the entire diseased area may consist of the latter color. Specimens are common in which the color of the spot on the seed is lighter, varying from drab to snuff brown or saccardo umber. The larger spots usually have a vinaceous buff to avellaneous-colored,

[2] The colors as given correspond to those given in Ridgway's *Color Standards and Nomenclature*, and, while characteristic, there is considerable variation from them.

often raised, center, which sometimes splits open disclosing the affected cotyledon. The spots may occur on any part of the seed coat, and may appear as a small black or brown speck or involve more than half the surface. In badly diseased seeds the lesion extends through the cotyledon and may even affect the embryo, but in many cases the cotyledon is but slightly or not at all discolored.

On the seedlings

Seedlings from badly diseased seed show blackened cankers on the cotyledons (fig. 10), in which, under moist conditions, small flesh-colored masses appear scattered over the surface of the lesions. The stem may become affected along its entire length, but usually it is affected only below the point of the attachment of the cotyledons. The first indication of a lesion is the appearance of brown specks in the epidermis. Later there appears a browning of the tissues lengthwise of the stem and below the epidermis. Still later, small pits appear along the affected area. Occasionally these cankers become so deep or so numerous that the stem is unable to support the parts above.

On the leaves

The leaves (figs. 10 and 11) not infrequently become badly affected. The lesions appear on the veins, usually on the underside of the leaf. These lesions have practically the same appearance as those on the stem. The tissues on each side of an infected vein and beyond it may wither and die. A considerable area of a leaf may become affected in this manner, giving it somewhat the appearance of blight. Usually only a small part of the leaf tissue is killed, and such places appear on the upper side as angular, elongated, dead areas, which sometimes become torn, giving the leaf a ragged appearance. The petiole may become so badly affected that it cannot support the leaf blade.

On the roots and other parts

The roots of plants growing in the soil are rarely if ever affected; but on seeds sprouted in a moist chamber, where the young roots are exposed, lesions similar to those on the stem may be produced by artificial inoculation. Muncie (1914: 4) mentions a rotting of the root due primarily to the anthracnose and blight organisms followed by secondary rot-producers

FIG. 10.—ANTHRACNOSE ON YOUNG BEAN PLANT SHOWING LESIONS ON JUVENILE LEAVES AND ON STEM
(Photographed by H. H. Whetzel)

FIG. 11. ANTHRACNOSE ON BEAN LEAVES

Lesions on the veins cause death of the mesophyll about them, and show as brown dead spots irregular areas on the upper surface of the leaves

The other parts of older plants may become diseased, and lesions similar to those already described may appear on the branches of the plant and on the pedicels, the sepals, and the bracts of the inflorescence. These parts of plants grown out-of-doors, however, become affected only during protracted periods of weather favorable for the organism.

On the pods

It is on the pods that the disease assumes its most striking appearance (Plate V). The first evidence of it there is the occurrence of tiny brown specks in the epidermis. These may be rufous or ferruginous, slightly elongated areas extending at an angle to the long axis of the pod. These specks enlarge to spots which become black at the center, with a vinaceous-rufous to hazel-colored border of varying width. These

black spots with colored borders are characteristic of anthracnose. The cankers range in size from a mere speck to spots one centimeter in diameter or even larger. By the union of several large cankers, a broad lesion is often formed which may extend from one end of the pod to the other. A canker may extend through the endocarp and even to the seed, particularly if infection takes place early, in which case the pod sometimes fails to develop and becomes shriveled and dried. Cankers resulting from infections that occurred during the later growth of the pod seldom extend below the endocarp. As the pod matures, the lesion is marked at the edge of a canker by a slightly raised, black ring with a cinnamon-rufous to chestnut-colored border. The center of the spot is then somewhat light buff in color. Flesh-colored spore masses on the surface of a young canker dry down to gray, brown, or even black granulations or to small pimples.

The appearance of the disease on the pods of the different varieties is very similar. The lesions on Blue Pod Butter, a variety producing dark blue-purple pods, are snuff brown instead of black in color; otherwise they are similar to those on other varieties. On a number of picked pods that had been left in a basket and were somewhat wilted, and in other cases in which inoculations were made, lesions one centimeter or more in diameter appeared which were light brown in color and marked by a slight depression. If the spores had not been present one would hardly have believed the lesions to be anthracnose, particularly as the typical lesions were present also on some of the pods. In some instances these unusual-appearing lesions later assumed the more characteristic appearance. Lochhead (1903) mentions the presence of a pink rot (*Cephalothecium roseum*) in anthracnose spots on bean pods, and at Ithaca this fungus has been found often in such lesions.

Blight lesions (Plate VI) on the pods may sometimes be confused with anthracnose. The blight lesion consists of an area having a water-soaked appearance extending along the dorsal suture, or of spots of a similar nature and of various diameters appearing on the sides of a pod. Often a pod may have many such discolored spots, these having originated from insect bites or punctures. The spots usually have an ochraceous-tawny center with a border of a cinnamon-rufous color, and commonly, as the pod matures, the entire lesion turns to hazel or to cinnamon brown with a more highly-colored margin. It may be distinguished from anthracnose by the absence of any dark color,[3] by the shape of the lesions which

[3] A saprophytic Alternaria may occur on blighted leaves and pods and give a blackened color to the lesion.

are usually more extensive and more irregular in outline than those of anthracnose, and by the absence of spore masses.

Rhizoctonia (Plate VII) often occurs on the pod, producing lesions which, particularly when they are small, closely resemble anthracnose. This fungus attacks only the pods lying in contact with the ground. The lesion has a bay to auburn center, often with a dark-colored ring near the margin surrounded by a ferruginous border. The lesions are more extensive than those of anthracnose, however, and do not contain the characteristic spore masses (Plate I).

Sclerotinia libertiana Fuckel produces a disease characterized by a soft brown rot and moldy appearance of the pod, followed by a shriveling and drying, which can never be confused with anthracnose. This fungus commonly produces rather large black sclerotia on the pods.

On pods of certain varieties, rust (Plate VIII) sometimes occurs as pustules containing a black mass of dusty spores.

When immature pods are exposed to the hot sun — as is often the case when the leaves are injured by blight or by other means, especially when the plants are approaching maturity — the exposed surfaces become discolored with brown specks, spots, or blotches, in some cases a little sunken, which may be mistaken for blight but hardly for anthracnose. MacMillan (1918) describes these lesions as he found them on certain varieties of beans in Colorado and in the East, and the writer has observed them commonly in the East on many varieties. A peculiar browning, different from sun-scald, was also observed, but the cause was not determined. A browning of pods may occur from other causes also, none of which, however, need be mistaken for anthracnose.

ETIOLOGIC ASPECTS

Name, classification, and synonymy of the causal organism

Bean anthracnose is known to be caused by the fungous parasite *Colletotrichum lindemuthianum* (Sacc. & Magn.) Bri. & Cav., one of the Melanconiales of the classification of Lindau (1900) as used in Engler and Prantl's *Die natürliche Pflanzenfamilien*. The fungus does not differ appreciably in its morphological characters from a number of other species belonging to this genus, nor, except for the presence of setae, from the genus Gloeosporium. Not only are species of the genus Colletotrichum

id of the related genus Gloeosporium similar in appearance, but so the diseases produced by species of the two genera are similar in aracter.

Saccardo (1878), in his description of the fungus, gave it the name *loeosporium lindemuthianum* Sacc. & Magn. after Lindemuth, who scovered the fungus in 1875. Scribner (1888:364) described the presence setae in the acervuli which were present on most specimens sent him om several States, and thought it probable that the generic name of e fungus should be changed to *Colletotrichum*. The following year riosi and Cavara (1889) named the fungus *Colletotrichum lindemuthnum* (Sacc. & Magn.) Bri. & Cav., and distributed it as such. The me year Scribner (1889), again finding setae in the acervuli, placed the ngus in the genus Colletotrichum and published it as *Colletotrichum ndemuthianum* (Sacc. & Magn.) Scribner. The name given by Briosi d Cavara stands, although it is evident from much subsequent cultural ork that the presence or absence of setae is not a character of sufficient ability to serve as a basis for the determination of generic position. ruger (1913:294–303) was able to develop setose and non-setose cultures this fungus at will, finding that a number of factors, such as age of the ulture, and nature and moisture content of the substratum, were control-ng agencies. He, however, designates the conidial form as *Gloeosporium* ubgenus *Colletotrichum*) *lindemuthianum* Sacc. & Magn.

Halsted (1893d), after making cross-inoculations on bean and water-elon, decided that the anthracnose fungi in these two hosts were the me, and used the name *Colletotrichum lagenarium* (Pass.) Ellis & Hal-ed, including in the synonymy the names that had been applied to the ganism causing melon anthracnose and bean anthracnose, respectively. ear and Wood (1913:46) found perithecia producing asci and ascospores cultures made from an anthracnose spot on a bean pod, and they refer eir fungus to *Glomerella lindemuthianum* Shear n. comb. Krüger (1913: 1), although he did not find perithecia, designates the fungus as *Glomerella ndemuthianum* Shear n. comb. Edgerton (1915:255–256) questions ether any perithecial stage of this fungus has ever been seen, and sug-sts that Shear and Wood might have been working with one of the prophytic forms occurring commonly on bean pods. He believes e fungus should be considered as a species of Colletotrichum until rther evidence supports a different view.

At various times other names have appeared in the synonymy of this fungus. Richon (1889) gives the name *Glaeosporium phaseoli* n. sp. to a fungus which he found on the pods and stems of beans at St. Amand, France. His meager description fits this fungus very well, and it is not improbable that he had before him the fungus causing bean anthracnose. Saccardo (1892) lists *Gloeosporium phaseoli* Rich. and gives Richon's description. Allescher (1903) also lists Richon's fungus and gives his description, but says that it is an uncertain species perhaps identical with *G. lindemuthianum* Sacc. & Magn. or with a Colletotrichum.

Allescher (1903) designates as *Gloeosporium lindemuthianum* Sacc. & Magn. forma *foliicolum* Allesch. the fungus he found on the upper surface of subcircular, brownish spots on leaves of *Phaseolus vulgaris* var. *nanus*. An examination made of type specimen No. 380 Allescher & Schnabl (1894), in the herbarium of the Pathological Collection of the United States Department of Agriculture, showed spots somewhat larger and more nearly circular than is usual for anthracnose but not sufficiently distinct to warrant the placing of the fungus as a form of the species. The spores are like those of *Colletotrichum lindemuthianum*. Allescher says the form *foliicolum* is similar to the type except in the appearance of the spots as described and in the absence of setae.

Desmazières (1843a) describes as *Septoria leguminum* Nob. a fungus on the pods of Phaseolus. He ascribes to variety "*b*" of the same species a form on Pisum. Saccardo (1878) says he is not able to decide whether or not *Septoria leguminum* Dsmz. should stand, as he cannot distinguish the young condition from *Gloeosporium lindemuthianum*, but the description varies widely from Septoria and approaches more nearly that of *G. fructigenum* Berk. Berkeley (1881), speaking of dried specimens distributed by Desmazières under the name *Septoria leguminum*, says the species shown is not a good representative of the genus Septoria, but belongs rather to Gloeosporium and has been figured by Saccardo in his *Fungi Italici* as *Gloeosporium lindemuthianum*. Cooke (1881), on the basis of Berkeley's observations, cites *Septoria leguminum* Desm. as synonymous with *Gloeosporium lindemuthianum* Sacc. Kirchner (1906: 137) ascribes to it the small, dry, sharply differentiated brown spots on beans, on which appear later very small black pimples.

Specimens of bean pods distributed by Desmazières (1843 b) as *Septoria leguminum*, deposited in the cryptogamic herbarium of the New

York Botanical Garden, show the presence of the fructifications of two fungi on one of the two pieces of pods in the packet. One of these, occurring in characteristic young anthracnose spots, has the typical spores of *Colletotrichum lindemuthianum* except that the average width, 5.75 μ, is a trifle greater. There can be no doubt that it is the bean anthracnose fungus. The other fungus appears on the specimen as numerous small black pycnidia and these contain typical Septoria spores. The other specimen shows only the Septoria-like fungus. Desmazière's description of the fungus given in *Annales des Sciences Naturelles* (1843a), and also accompanying the specimen, is of the Septoria, but his description of the disease applies, at least in part, to the condition produced by the Colletotrichum. This probably led to the mistake of ascribing to *Septoria leguminum* Desm. the anthracnose present on pods of *Phaseolus vulgaris* distributed by Von Thümen (1882) as *S. leguminum* and by Roumeguère (1884) as *S. leguminum* Desm. var. *Phaseolarum*. Saccardo (1896) describes a fungus, which he names *Gloeosporium socium* Sacc., as occurring on the leaves of living bean plants (*Phaseolus vulgaris*). But from his description it seems improbable that he has the bean anthracnose fungus. D. Saccardo (1904) labeled as *Colletotrichum lindemuthianum* (Sacc. et Magn.) Cavara f. *brachysporum* specimens of a fungus on bean pod, *Phaseolus vulgaris*, the conidia and basidia of which were recorded as considerably shorter than the normal average. An examination of type specimens in the herbarium of the New York Botanical Garden shows small but typical anthracnose spots, from which, however, no spores were obtained.

Heald and Wolf (1911) have ascribed to a new species, *Colletotrichum caulicolum*, a destructive canker which they found on the stem of Kentucky Wonder beans in Texas. They say that this fungus differs from *C. lindemuthianum* in that the setae are produced abundantly in the host and that the spores are larger and are falcate. Their description of the disease and of the fungus is similar in most respects to that of bean anthracnose and its pathogene, but it is not possible from the description to decide that the fungi are the same. Cooke and Harkness (1880) report *Gloeosporium leguminis* C. & HK. on legumes in California, and later (1884) on pods of Robinia at Sacramento, California. Cooke (1880) describes *Discella leguminum* Cooke on the pods of Prosopis found in Texas. Comes (1891) lists *Discella leguminum* Cooke and *Gloeosporium leguminis* C. &

Hark. as synonyms of *Gloeosporium* (*Colletotrichum*) *Lindemuthianum* Sacc. & Magn. An examination of type specimens of these two fungi in the possession of Dr. C. L. Shear, of the United States Department of Agriculture, leads to the conclusion that they are not at all related to the fungus here considered.

The synonymy would, then, appear as follows:

Gloeosporium Lindemuthianum Sacc. & Magn. Michelia 1:129. 1878.
Septoria leguminum Desm. *In* Von Thümen, Mycotheca universalis, no. 2096. 1882.
Septoria Leguminum Desm. var. *Phaseolarum*. *In* Roumeguère, Fungi gallici exsiccati, no. 2791. 1884.
Colletotrichum lindemuthianum (Sacc. & Magn.) Bri. & Cav. I funghi parassiti delle piante coltivate od utili, no. 50. 1889.
Colletotrichum lindemuthianum (Sacc. & Magn.) Scribner. Orchard and garden 11:193-194. 1889.
? *Glaeosporium phaseoli* Ch. Rich. Cat. raison. champ. Départ. Marne, p. 401. 1889.
Colletotrichum lagernarium (Pass.) Ellis & Halsted. Bul. Torrey Bot. Club 20:246-250. 1893.
Gloeosporium Lindemuthianum Sacc. & Magn. forma *foliicolum* Allesch. *In* Allescher and Schnabl, Fungi bavarici exsiccati, no. 380. 1894.
Colletotrichum Lindemuthianum (Sacc. et Magn.) Cavara f. *brachysporum*. Mycotheca italica, no. 1364. 1904.
Glomerella lindemuthianum Shear n. comb. *In* Krüger, K. biol. Anst. Land- u. Forstw., Arb. 9:311. 1913.

Morphology and physiology

Spores

Whether the fungus is grown on its host or in culture media, the spores are produced abundantly on the surface in acervuli masses of a grenadine pink color. Frank (1883 b:513) mentions the presence of a slimy substance with the spores in the acervulus, and this has since been noted by other workers as a gelatinous substance in which the spores are embedded. If such a mass of spores is placed in water, they separate and become suspended in the water so that they are readily disseminated by its dispersal. If the acervulus remains dry, it hardens and shrinks down to small gray or brown granulations, and the spores are seldom set free under such circumstances.

The summer spores (conidia) are oval or oblong, cylindrical, one-celled bodies of somewhat variable size (Plate III, 1). They are straight or slightly curved, with the ends rounded or at one end somewhat pointed. The dimensions, as averaged from a large number of spore measurements, are 15 by 5 μ. The largest spore encountered measured 22 by 5.33 μ and the smallest 13 by 4.44 μ. The content of young spores is homo-

geneous and granular. Often there is a clear body resembling a vacuole near the center, which Edgerton (1910:20) describes as a nucleus but which earlier workers have regarded merely as a vacuole. Edgerton says that as the spore ages it becomes vacuolate, and finally the contents collect in small masses. The spores are no longer viable when this last stage is reached.

Spore germination

In making germination tests, spores from young acervuli produced in bean-pod cultures were transferred to a drop of the culture medium placed on a flamed slide. The slides were transferred to sterile moist chambers or petri dishes kept moist with wet blotting-paper, in which they rested on glass supports to hold them up from the bottom. The temperature was maintained at about 20° C.

Germination usually takes place by the protrusion of a germ tube from the side of the spore near one end and at an angle to its long axis. On nutrient media some spores have germinated within eight or nine hours (Plate III, 2). Bean agar gives the quickest and largest percentage of germination, although nutrient beef agar, potato agar, and beef bouillon give nearly similar results. Soon after the protrusion of the first tube, a second may be sent out from a similar point at the other end. As many as four germ tubes have been observed coming from a single spore, but rarely are there more than two. Dey (1919:307) observed in a few cases more than two germ tubes developing from a spore. The germ tubes form branches which radiate from it in all directions (Plate III, 4).

Germination takes place more slowly in water than in agar. A few spores were observed to have germinated in water after eighteen hours (Plate III, 10). In certain rain-water cultures about one-half of the spores germinated in twenty-four hours, but this was a greater proportion than the average. In distilled water, germination proceeded somewhat more slowly. The majority of the spores in these water cultures became uniseptate during germination, but septation was not observed to occur so commonly in spores germinating in nutrient solutions. Often there is a constriction of the spore at the septum. In some cases the spores themselves increased somewhat in size before or during germination, but this was not general and when spores were placed in nutrient solutions

it did not occur to any extent. Atkinson (1895) says that septation occurs unless the spore is very short, and that the spore becomes constricted at the point of septation soon after germination. He observed an increase in the size of the spores after germination until they became several times larger than at first, and states that even with spores which fail at first to germinate a similar increase in size takes place, and they become uniseptate, strongly constricted at the septum, and richly charged with highly refringent granules. Edgerton (1910:19) states that the spores swell but slightly or not at all in germinating in nutrient media if they are scattering, but if they are abundant and close together in the culture medium they swell to two or three times normal size in some cases. During the process of enlargement a septum is formed, and with further swelling a constriction of the spore appears at this point. Edgerton finds that "when there are more than 12 or 15 spores to the cubic millimeter of medium, the spores become swollen, germinate slowly and but poorly. When the number is less than this, they germinate with but little, if any, swelling" (page 20 of reference cited). He thinks this may be due to an enzyme prohibiting growth, given off by the spore during germination. Dey (1919) observed that if the drop of water used in the culture had a convex surface, the spores lying in the middle hardly germinated while most of those at the border did. He thinks this difference is due to a difference in the oxygen supply.

The germination of the spore in water consists, in most cases, of the production of an appressorium at one or both ends of the conidium (Plate III). This is a subglobose body flattened on one side, having dark-colored, thick walls and containing dense granular protoplasm. It often appears attached directly to the conidium or is produced at the end of a short germ tube, although it is not uncommon to find an appressorium at the end of a long, narrow hypha. In the ordinary process of germination in nutrient media, the spore contents become coarsely granular and the vacuole increases greatly in size or there may be several vacuoles. In rain-water cultures, the spore contents during germination seem to pass into the appressorium, in which the protoplasm appears to be very dense.

The appressoria in most cases are closely appressed to the slide. A few have been noticed, however, which were apparently free, as they were observed to move when the slide was jarred. In the course of twenty-four

hours some of these appressoria themselves send out a slender germ tube, at the end of which in most cases another appressorium is formed. After nine days about 50 per cent of the spores in this experiment had germinated but had not proceeded much beyond the production of appressoria. A number of spores had the appearance of being empty, and other peculiarities were noticed to which no importance could be attached.

Frank (1883b:513–515) describes the germination of the spore and the formation of appressoria, he being the first to apply the name to these bodies. These appressoria, Frank says, come to have a thick, irregular, dark purple membrane. They are produced abundantly when spores are germinated on the surface of bean or cucumber tissue, but seldom occur when germination takes place in water on a glass plate. Instead, long, thin, germ tubes are formed, at the end of which a small appressorium may appear, or the spore may produce another spore or sporidium attached directly to the spore or to a short tube. Frank says the appressoria do not germinate unless they are in contact with the host. He thinks their production is stimulated by the quality of the substratum, and suggests that their function is to prepare the fungus for penetration into its host plant.

Appressoria are produced by other Gloeosporia of the Glomerella type, and their significance has been discussed by other writers. Halsted (1893a 305) suggests that they may be formed as a protective body to tide the germinating spore over unfavorable periods. He says that, while the appressorium is often a single cell, it may become an aggregation of thick-walled cells like a sclerotium. He thinks the appressoria may be of taxonomic value. Stoneman (1898:113) does not find them to occur as a constant character, but thinks they may be forced in certain species by lack of nourishment. Hasselbring (1906:142), from studies of *Gloeosporium fructigenum* Berk., believes them to be adhesion organs during early stages of infection, and thinks they are formed as a result of contact stimuli of the germ tube but lose this power of reacting in nutrient media. He calls attention to the presence of a germ pore in the flattened side, through which the germ tube protrudes during germination. He finds the appressoria much more resistant to desiccation than the spores. Edgerton (1910:21) finds appressoria produced in nutrient media, often not in contact with the glass or any solid substance; and in this species, *Colletotrichum lindemuthianum*, the "germ pore" is often lacking.

Gardner (1918:21), in his spore-germination studies of *Colletotrichum lagenarium*, concludes that a rather abundant supply of oxygen and a contact stimulus is necessary for appressorium formation, and that the presence of food material does not seem to inhibit such formation. Dey (1919), in his studies of *C. lindemuthianum*, states that appressoria are formed whenever the germ tube comes into contact with a hard foreign substance which acts as a stimulus for their formation. He found no germ pore in the appressoria observed, but noted that the germ tube arose from the side in contact with the glass. He observed the appressorium to be sheathed in a mucilaginous coat, which aids it in becoming attached to a foreign substance so firmly that even a jet of water fails to dislodge it.

In all the cultures made in fresh nutrient media, the germination was rapid, the germ tubes were as large, or nearly so, as the spores, few or no appressoria were formed, and the subsequent development of the mycelium was luxuriant; while in water cultures, the germination was slow, the germ tubes were much smaller in diameter, the production of appressoria was abundant, and subsequent development of mycelium was scanty or there was none at all. It is true that appressoria were commonly produced in nutrient media that was becoming somewhat dry and hard, as occurred soon when only a little was poured into a petri dish. When a nutrient medium is poured over a water culture, as suggested by Hasselbring (1906), the appressoria germinate within a few hours and produce a rich mycelial growth.

Mycelium and spore production in culture

Under favorable conditions for growth, the germ tube branches to form hyphae, and these in turn, by further growth and branching, develop within forty-eight hours into a mycelial mat often one millimeter in diameter. In three or four days conidia are produced at the ends of the hyphal threads. In several agar cultures in this experiment they were produced abundantly on short threads within twenty-four hours. They are formed by the constriction of the wall near the extremity of the hypha. A spore thus formed is pushed aside and the hypha elongates to about the same point, when constriction again occurs. In this way several spores are formed from a single branch, and can be seen lying side by side or piled in a heap at the end of the branch (Plate III, 5). Atkinson (1895:309) observed conidia being produced directly on the

ore, and in the writer's cultures this condition was frequently met. tkinson found that the ends of the hyphal threads have a dichotomous ppearance, due to a branch just behind the growing end overtaking e primary thread, and that a plumose tuft is produced by this dichotoous branching taking place successively in the same thread.

The mycelium, which at first is white, will become dark-colored after growth of several days in a starch-containing medium. This is especially oticeable with the growth in potato agar and bean agar and on sterilized an pods. A culture four or five days old shows a dark center with ire white mycelial growth at the margin and aërial mycelium developing er the surface. As growth continues, dark-colored knots of mycelial reads appear scattered from the center outward, and above these darker rts of the culture, flesh-colored masses of spores (acervuli) begin to produced if the culture is in good condition. Dey (1919) finds that cornmeal agar cultures these spores are surrounded by small dark ines. On sterilized bean pods inoculated with spores kept at a temrature of about 22° C., there is a rapid growth of mycelium which in o days begins to darken and after three days produces spores in acervuli. six days the pod is covered with a pale salmon or pale flesh-colored ass of spores. Cultures kept for a long time or at unfavorably high mperatures lose their power to develop spores in this way when transred to fresh media. Commonly they develop only a slow growth of ite mycelium. Spores will usually be produced if the mycelium turns rk.

Viala and Pacottet (1905), from a study of *Colletotrichum lindeuthianum* in culture, report the production of spermagonia, pycnidia, sts, yeasts, and sclerotia, as well as conidiophores, similar in most spects to those produced by *Manginia ampelina*, another fungus under eir observation. Shear and Wood (1913:64) say yeasts have never curred in their cultures of Gloeosporia except where they were evidently ntaminations, and they have never observed the production of spermagonia or pycnidia by these fungi. No other writers in speaking of *lindemuthianum* or related forms have mentioned the production of dies of these kinds, except that Edgerton (1910:10) reports having en found pycnidia-like bodies in the tissue of the bean seed.

Temperature is an important factor in the development of the fungus connection with its host or in culture media. Edgerton (1910:29)

found that the fungus died in culture at Baton Rouge, Louisiana, during the summer, even when frequently transferred to fresh media, and later (1915) showed that the temperature requirements for this fungus are lower than for other anthracnose fungi, the optimum being about 22° to 23° C. though there is but little difference in growth between 19° and 26°. Edgerton gives the maximum as about 30° or 31° C. The growth at optimum temperatures is between 3 and 4 millimeters a day. Muncie (1917:9–11), after subjecting test-tube cultures of old mycelium to a water bath at 65° C. for ten minutes, found that good growth could yet be obtained but that the thermal death point of young mycelium lies between 50° and 52.5° C. and that of spores between 45° and 48° C.

The writer endeavored to determine the minimum, optimum, and maximum temperatures for growth and production of spores. Potato-agar plate cultures of two physiologically different strains of *Colletotrichum lindemuthianum* were kept for a few days at 25° C., after which blocks of agar 3 millimeters in diameter of each strain were transferred to plates of potato agar and corn agar and to tubes of sterilized bean pods. The temperatures (centigrade) at which the cultures were placed were, respectively, 0°, 4°, 10°, 16°, 22°, 28°, 34°, 40°, 43°. Two cultures of each strain in potato agar and two of each in corn agar were placed at each of these temperatures on April 8, 1914. The growth made by them is shown graphically in figure 12.

It is seen that the average growth during the first six days was less than on the eight succeeding days at the temperatures 4° and 10° C. but was greater at temperatures above 28° C. Growth was probably checked during the first day or two at the lower temperatures by an abrupt transfer from a warm room, but was resumed to some extent later. While the growth was no doubt checked by the transfer to the higher temperatures, and ceased altogether after a few days at 34° and above, yet some growth was possible during the first day or two because the temperatures then ranged between room temperature, at which the cultures were started, and the higher temperatures. The figures giving the average growth on the eight days following the first six represent more nearly accurately the actual growth that occurs at these temperatures under these conditions. Considering, then, the curve representing such growth, it appears that the minimum temperature for growth lies at 0°, the optimum at 22°, and the maximum at 34°. As a matter of fact, the

minimum lies somewhere between 0° and 4° C., the optimum near 22°, and the maximum between 34° and a few degrees lower. This corresponds very closely to the observations of Edgerton (1915:254). The corn agar permitted a little better growth than the potato agar.

The growth at 4° C. was white, with considerable aërial mycelium in most cultures. After four weeks a growth of from 25 to 35 millimeters

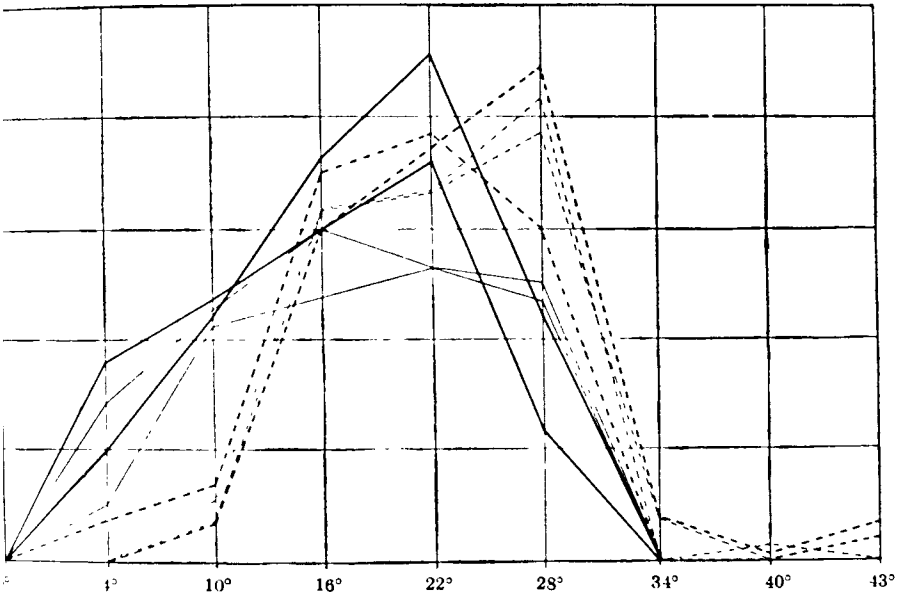

FIG. 12. CURVE OF GROWTH OF TWO STRAINS, A AND B, OF COLLETOTRICHUM LINDEMUTHIANUM AT VARYING TEMPERATURES

The light curves represent growth in potato agar, the heavy curves growth in corn agar. The dotted lines represent average growth per day during the first six days, the straight lines, average growth per day during the following eight days. The temperature is expressed in degrees centigrade

was attained, and an olivaceous color, with spore production, was noticed in a few agar and bean-pod cultures. Spores were produced in abundance on bean pods at 10°, 16°, and 22° in six days, and but sparingly at 28°. As already stated (page 121), bean pod cultures kept at 22° C. have been found to give a rapid and abundant production of spores when the fungus was in a spore-producing condition, in hundreds of cultures made by the writer.

The relation of growth of this fungus to acid and alkaline media has not been studied by the writer, though he has observed that not a good growth is secured when the fungus is cultured in a potato-agar medium made acid by the addition of one drop of 50-per-cent lactic acid to 10 cubic centimeters of medium, as when such acid is not added. Edgerton (1910:28) records a fair growth of *Colletotrichum lindemuthianum* at −16 Fuller's scale, excellent growth at +5, and only slight growth at +20. *Glomerella gossypii* (South.) Edg. grew better than did *Colletotrichum lindemuthianum* in the more acid media.

The ascogenous stage

The ascogenous stage of many anthracnoses has already been found in nature or produced in culture. Klebahn (1905) has shown that the Gloeosporium causing sycamore anthracnose is a Gnomonia. He also (1907:65) found the perfect stage of *Gloeosporium ribes* (Lib.) M. & D. causing an anthracnose of currant leaves, to be a Pseudopeziza. Burkholder (1917:164) discovered the perfect stage of *Gloeosporium venetum* Speg. on raspberries to be a Plectodiscella, which he named *P. veneta* Burkholder. Genera representing perfect stages of other Gloeosporia that have been reported (Stevens, 1913) are Glomerella, Gnomoniella, Gnomonia, Trochila, Physalospora, and Calospora. Most of the anthracnose fungi parasitic on fruits and herbaceous plants, including the one on bean, belong to what is known as the Glomerella type, that is, their perfect stage when found is of the type of the genus Glomerella. Even in their imperfect stage they differ somewhat from the other forms. Edgerton (1908:384) has pointed out the following important differences, among others of minor importance:

Glomerella type	Gnomonia and Pseudopeziza types
Spores oozing out as a pink mass	Spore mass white, cream-colored, or yellow
Appressoria produced in certain cultures under certain conditions	No appressoria observed
Mycelium in culture varying but little in diameter	Mycelium in culture varying in diameter (at least in Gnomonia type)

Stoneman (1898:99–112) was the first to discover the ascogenous tage of a Glocosporium of the Glomerella type, and she described five pecies occurring in nature or in culture. These were placed in a new enus of the Gnomoniaceae which Stoneman named Gnomoniopsis. Since hen the perfect stages of at least thirty-two other Gloeosporia or Colle-otricha have been found in nature or produced in culture. Von Schrenk nd Spaulding (1903), because of a prior use of the name Gnomoniopsis, ubstituted for it the name Glomerella.

Shear and Wood (1907, a and b, and 1909) have produced in culture ie perfect stage of anthracnose fungi from a large number of hosts, and nong them what they believed to be the ascigerous perithecia of *Colleto-richum lindemuthianum*. They say that light, temperature, and moisture re not factors of much importance in producing this stage. They hold hat once a race, a strain, or a generation is obtained that will produce he perithecia, these may be produced in various media and under diverse onditions. Moreover, they state that if a given strain will not produce erithecia in sterilized cornmeal at 75° to 85° F., it is useless to try longer o obtain them from that strain. In a later publication (1913:14), after aving studied forms on forty-five different hosts and having obtained ie ascogenous stage from thirty-six hosts, they refer forms from thirty-ine hosts to *Glomerella cingulata* (Stonem.) S. et v. S., the one from otton to *Glomerella gossypii* Edg., the one from bean to *Glomerella* [illegible] *Shear*, those from watermelon, cucumber, and squash o *Glocosporium lagenarium* (Pass.) Sacc. & Roum., and the one from anana to *Glocosporium musarum* Cke. & Mass.

In the same publication (1913:46–47) Shear and Wood record the nding of perithecia producing asci and ascospores in flasks of cornmeal om cultures made from an anthracnose spot on a bean pod. While ie perithecia were abundant, conidia were scarce or wanting. Numerous ubsequent plate cultures made from crushed perithecia and asci and from ngle ascospores produced the usual growth of mycelium and abundance perithecia with mature asci, but no conidia were seen. Shear and Wood elieve this form to be an extreme variation of a condition they have oticed in respect to cultures from other hosts, in that cultures from scospores produce fewer conidia than do cultures made from conidia. Edgerton (1915:255) thinks it doubtful that any perithecial stage f *Colletotrichum lindemuthianum* has ever been seen, and that Shear

and Wood were not working with a culture of the true bean-anthracnose fungus but rather with one of the saprophytic forms which Edgerton finds occurring commonly on old parts of bean and other plants. These forms produce perithecia abundantly, but no conidia. In hundreds of cultures of *C. lindemuthianum* examined by him, no perithecia have been found, and he thinks that until more satisfactory proof is offered of the presence of perithecia it is better to consider the bean anthracnose fungus as lacking an ascogenous stage.

Relation of fungus to host

Penetration of the host

Frank (1883b:515) described in detail the germination of the spore and the penetration of the host. He says that the spore, on germinating, produces a germ tube, which on coming into contact with the epidermis of the host forms an appressorium closely pressed against the surface of the epidermis. This either remains unchanged, or after a time becomes thinner and colorless on one side, and from this spot a germ tube appears. The germ tube penetrates directly through the cuticle into the epidermal cell, and either fills this cell with branching hyphae or quickly penetrates the adjoining epidermal cells or those beneath. Voglino (1892), from inoculations of parts of green bean pods, observed the germination of the spore, the quick formation of large numbers of appressoria, and the production of mycelial filament which penetrated into the interior of the epidermal cells. Dey (1919) has carefully studied and figured this penetration from stained sections made from material embedded in paraffin. He finds that a peg-like infection hypha grows out from the surface of the appressorium in contact with the host, which mechanically ruptures the cuticular layer and then brings about a swelling and disintegration of the subcuticular layers — probably by enzymic action. The infection hypha was never observed earlier than forty-eight hours after inoculation. The rupture of the cuticle is the result of the pressure exerted by the development of the infection hypha. This hypha is very fine at first, but reaches a normal size while growing in the cellulose layers below the cuticle. Here, or farther on in the cell, it produces a small vesicle from which one or more branches arise and extend into the host tissue. As the invading hypha enters the cell, the protoplasmic contents collect around it, and later a collapse of the cell takes place. The writer has never observed this

penetration. It seems that this is the really critical time in the development of the fungus, for it must overcome the protoplasm of the host cell before it can continue its development. Varieties of beans immune to certain strains of *Colletotrichum lindemuthianum* probably owe this immunity to the inability of the infection hypha of the fungus to overcome the resistance offered it by the protoplasm of the host cell. The writer (Barrus, 1918:594) has shown that some such varieties, on inoculation with such a strain, have shown on their pods and stems a slight but distinct specking, as though the fungus had entered the tissue and killed a few cells but was unable to proceed farther. This specking did not appear on the pods of plants not inoculated.

Once the fungus has established itself within the host cell, the hyphae extend horizontally and diagonally into other cells, penetrating the cell walls of the host as they come into contact with them (Plate II). In some cases the hyphae enlarge when in contact with the cell wall, and a small hole is formed through which projects a slender tube that at once enlarges after passing through. As many as twelve hyphae have been observed penetrating a single cell (Plate II, 4). Growth within the host is rapid, particularly if the tissue is young and tender. The protoplasm of the host cell is killed and turns brown soon after being attacked. The walls collapse, and after from four and one-half to seven days a lesion may be observed on the surface.

There seems to be a great difference of opinion as to the length of the period of incubation. Frank (1883a:33) noticed the beginning of a browning of the epidermis at separate points on the pods twenty-four hours after inoculation was made. This browning had extended by the following day, and five days after inoculation Frank obtained the first spores in the new lesion. Scribner (1888) states that the cells become discolored almost at once after the hyphae enter. Halsted (1892:284) found a spot on an otherwise healthy pod thirty-six hours after inoculating it in the laboratory under the most favorable conditions. Pammel and King (1909) report having obtained an anthracnose spot thirty-six hours after inoculation. Dey (1919) claims that early specking appears on a pod when tap water is substituted for infection drops, and thinks it due to osmotic disturbances. Edgerton (1910:14) finds from inoculations made on plants in the greenhouse and in the field that the period of incubation ranges from four and one-half to nine days, depending on the

weather and on temperature conditions. The writer's numerous observations are in accord with this as regards the production of typical anthracnose lesions. Temperature appears to have some influence on the length of the incubation period; also, the period varies considerably with the different varieties of beans under the same conditions. Schaffnit (1920) finds that the incubation period, and also the period between infection and spore formation, differ with different varieties.

Reproduction of the fungus within the host

At about the time when the cell walls collapse to form a canker, or even earlier in many cases, the mycelium at certain points develops abundantly in the epidermal cells and in those just beneath, forming a stroma of closely crowded, many-septate hyphae. The host cells at these places are so flattened that it is difficult to observe them (Plate II, 2). From this pseudoparenchymatous tissue arise short, more or less erect conidiophores, from 15 to 20 μ long and from 4 to 5 μ broad, at the apex of each of which is borne a small conidium rounded at the top and drawn out to a point at its attached end. This conidium enlarges somewhat before becoming detached. The conidia are formed by the constriction of the upper end of the conidiophores, as described in connection with germination in culture media. Spore after spore is produced by the conidiophore; the cuticle, which has been pushed up to form black pimples in the canker as the conidiophores elongate, is soon ruptured, and the spores emerge in a gelatinous pink mass (Plate I, 1). Frank (1883b: 513) describes the formation of the stroma and the production of spores enveloped in slime, the rupture of the cuticle, and the behavior of the spores thereafter.

These first acervuli formed at the center are followed by the production of others as the lesion enlarges. In a single lesion there may be fifty or more acervuli, in which thousands of spores are produced. Edgerton (1910: 12) estimated that on a badly spotted pod, from 110,000,000 to 115,000,000 spores had been produced. After washing these off and placing the pods in a moist chamber for twenty-four hours, he found that about 50,000,000 more spores were produced, and he concluded that a total of from 500,000,000 to 1,000,000,000 spores may develop on some pods. If the weather remains moist and cool, the conidiophores will continue to produce conidia; but during dry weather the spore masses harden down over the acervulus and spore formation ceases.

As the acervuli become older, long-pointed, brown, septate hyphae (setae) are produced here and there among the conidiophores and often in a ring near the margin. These range in length from 30 to 90 μ. Some taper evenly to a point from a base 8 to 10 μ wide; others have a bulbous base, which Beach (1892:319) reports as being often many-celled; many do not taper evenly but are swollen near the septa. They vary in number from a few to as many as twenty in an acervulus (Plate I, 2). Black stromata made up of dark-colored hyphae are produced on the surface of dead areas of leaves spotted by anthracnose and on the surface of dry pods, and these invariably support setae. Setae are abundantly formed also in old agar and bean-pod cultures. Frank (1883b:517) found them in lesions on bean pods, and describes them as sterile, brown, hair-like appendages of the fungus.

The fungus in the seed

The fungus passes the winter in the seed as mycelium lying within the cells in a more or less dormant condition. It may be confined to the cells of the seed coat, but in badly diseased seeds it occurs in the cells of the cotyledon. It exists there as vacuolate, closely septate, hyphae, from 3 to 5 μ in diameter, which are wound about in the cells or extend diagonally across into other cells. It may occasionally be found as a cobwebby growth between the seed coat and the cotyledon, or even between the two cotyledons within the seed. Frank (1883b 520) found spores produced in lesions of the seed, Scribner (1888) says that spores and basidia may be found between testa and embryo, and Halsted (1892:285) found them borne in the cavity between the cotyledons of the diseased dry seed. Halsted called attention to the rapid growth of the fungus and to the production of spores on the diseased seed when it is placed under a bell jar. Edgerton (1910:10) notes that acervuli are often present on the surface of the spots and between the cotyledons, and finds peculiar closed pycnidia-like bodies buried some distance beneath the surface of the bean.

Gain (1898) has shown that the density of attacked seeds may be lowered as much as 4.7 per cent. Muncie (1917:37) states that badly affected seed will remain on the surface of a solution of sodium nitrate of given concentration, while slightly affected and clean seed will sink in it.

The viability of the seed also is affected according as the mycelium has or has not penetrated beyond the epidermis which protects the embryo. Gain (1898 and 1899) says that 10 per cent of the affected seed planted did not germinate, 8 per cent germinated but did not grow, and 36 per cent, although affected, were viable; while 46 per cent having only the integument but not the cotyledon affected produced healthy plants, as the fungus cannot produce fructifications unless it has penetrated into the cotyledon. Seed affected to one-twentieth of their volume are not viable. Gain says also that the disease can be quickly communicated from one seed to another by contact, or by inoculation with spores. Halsted (1892) states that only half of the diseased seed germinated, and those that did germinate produced plants of a sickly nature. Observations made by various other workers seem to prove that affected seed germinates poorly. The experience of the writer indicates that the percentage of germination of anthracnose-affected seeds is dependent mainly on the tissue affected and the area of the lesion. If the embryo or the tissues near it are affected, the seed usually will not germinate. When conditions are far from optimum for germination of bean seed, affected seeds often do not germinate, but neither will healthy seed germinate well under such conditions. The larger proportion of plants appearing from healthy seed than from affected seed under unfavorable conditions for germination is due to the attack of the new tissues by the anthracnose fungus and sometimes by other fungi associated with it. Edgerton (1910:36) obtained a much lower percentage of germination from anthracnose-spotted seed planted in unsterilized soil than from that planted in soil that had been sterilized, due to rot organisms in the unsterilized soil which attacked such seed. He says, however, that in the latter case the great majority of plants appearing were destroyed by anthracnose, while in the former there was greater freedom from the disease, indicating to him, as did other trials and observations, that rot organisms of the soil, especially a certain Fusarium commonly associated with anthracnose spots on seed after planting, will in Louisiana greatly reduce the severity of the anthracnose.

It appears that when a diseased seed is placed in a fairly moist situation, the threads of the fungus, theretofore dormant, renew their activity, extending into healthy cells beyond and forming spore-bearing conidiophores at the surface of the lesion. These conidiophores appear first as small black pimples in the lesion, from which spores issue in small,

pinkish, pasty masses. As already mentioned, if the acervulus remains dry these spores harden down to little gray or brown granulations, and the spores are seldom set free under such circumstances. Ordinarily the lesion becomes wet with soil moisture or later with rain or dew, and then the spores separate from one another and become suspended in the water. Sometimes the entire seed becomes enveloped by a moldy growth of the fungus and fails to germinate; but when a diseased seed is viable and soil conditions are favorable, spores may be produced in the diseased parts of the cotyledons by the time they have appeared above ground. If the soil is sufficiently moist as the seed is emerging from the ground, spores are set free and these are able to infect the young and tender stems.

Infection of the seedling from affected seed

The plumule, consisting of the young leaves, is during germination and for a short time thereafter in intimate contact with the cotyledons (fig. 13). The water containing the suspended spores, by capillarity and

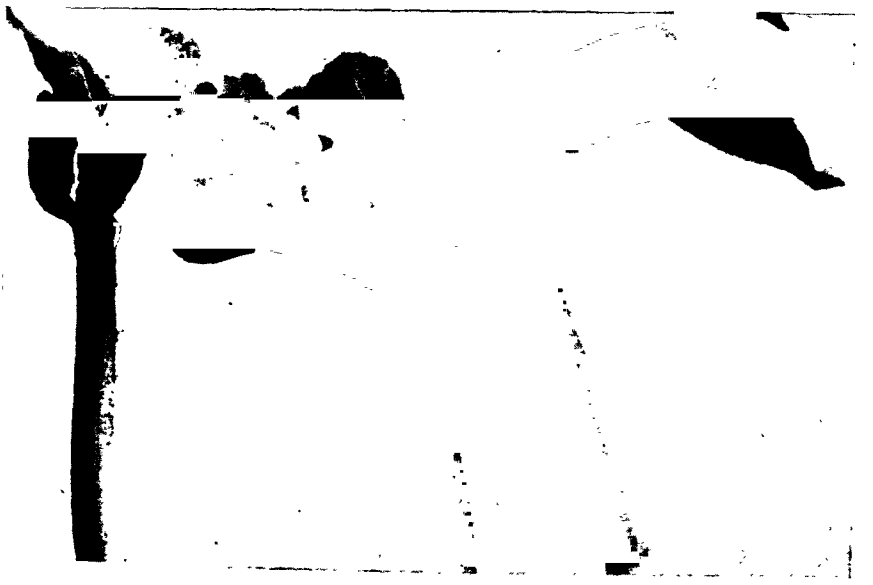

FIG. 13. SEEDLINGS PHOTOGRAPHED TO ILLUSTRATE MANNER OF INOCULATION OF JUVENILE LEAVES FROM SPORES PRODUCED ON COTYLEDON
Seven-eighths natural size

in other ways comes into contact with the now exposed under surface of these leaves. The stem may also become inoculated with spores that have been washed down from the cankers on the cotyledons, especially the base of the stem just below the surface of the soil, where moisture conditions are favorable for the germination of the spores. Frank (1883b:522) says that after affected cotyledons fall from the growing seedling, the fungus continues to grow in them and produces spores in great abundance which are washed by rain into the soil and bring about an infection of the plant in this way. Spattering of contaminated water and of soil also serves to inoculate the seedling; this is discussed more fully later.

Dipping seed in a suspension of spores just before planting will bring about an infection of the cotyledons and other parts of the seedlings, as has been shown by Edgerton (1910:41) and verified by the writer. Gain (1898) proved that the soil can become contaminated and serve as a source of inoculum.

Seeds planted in soil to which water containing spores of this fungus is applied will also produce infection. On August 22, 1910, thirty-six clean bean seeds were planted in twelve pots and watered with a suspension of spores of *Colletotrichum lindemuthianum*. As a check, six seeds were planted in two pots to which water without spores was applied. On September 6 thirty-one plants had appeared in the twelve pots, of which thirty, or 96.8 per cent, were infected. None of the six plants that appeared in the check pots were affected. On August 30, 1910, fifty clean seeds of the variety Golden Refugee were planted in a flat in clean soil, and water containing spores of *C. lindemuthianum* was poured over the surface until the soil was wet. On September 9 forty-nine plants had appeared, of which six showed anthracnose lesions. No later observations were made.

Longevity of fungus in soil

In order to find out whether spores washed to the soil would remain viable over winter, the following experiment was carried out. On November 27, 1916, twenty-five 8-inch pots were filled with loam and sterilized in the autoclave for three hours at twenty pounds pressure. On December 15, fifty test-tube cultures of *C. lindemuthianum* grown on

sterilized bean pods were placed in 4 liters of tap water and the spores were washed off. The suspension was then filtered through a mat of absorbent cotton to eliminate fragments of plant tissue. Twenty-one pots of soil were inoculated by pouring over the surface of each about an equal portion of the suspension. There being some of the suspension left over from the first application, a double portion was applied to three pots. Four pots did not receive any spores, and these were labeled *Checks*. Several thicknesses of cheesecloth were tied over the top of each pot and the pots were placed outdoors. In the course of the winter and spring, the pots were taken into the greenhouse and planted with Davis White Wax, a susceptible variety, the seed used having come from healthy pods and having been carefully sorted. Twenty-five seeds were planted in each pot. After the beans were planted, unused sphagnum was placed over the surface to the depth of an inch to keep the surface of the soil in a moist condition. At the last trial, on June 8, four of the pots were inoculated again with a fresh suspension of spores as a control. The results are given in table 3. It was thought that the pots planted on

TABLE 3 RESULTS OBTAINED BY GROWING BEANS IN SOIL THAT HAD BEEN INOCULATED WITH A SUSPENSION OF SPORES OF COLLETOTRICHUM LINDEMUTHIANUM, AS COMPARED WITH THOSE GROWN IN UNINOCULATED SOIL

Date of planting	Date of examination	Type of inoculation	Number of plants appearing	Number of plants affected	Remarks
Dec. 15, 1916	Jan. 6, 1917	2 single	25	11	Small lesion at base of stem
			25	2	Ditto
Jan. 30, 1917	Feb. 25	1 double	21	17	Well-defined lesions on stem
		1 single	24	2	Ditto
		1 check	23	0	
April 14	May 7	2 double	25	0	
			24	0	
		3 single	24	0	
			25	0	
			25	0	
		1 check	24	0	
Pots replanted May 7	May 29	2 double	25	4	Well-defined lesions on stem. All 4 affected plants adjoining
			24	0	
		3 single	22	0	
			22	1	1 small lesion on stem
			24	0	
		1 check	24	0	

TABLE 3 (*continued*)

Date of planting	Date of examination	Type of inoculation	Number of plants appearing	Number of plants affected	Remarks
June 8	June 24	8 single	23	0	
			24	1	5 old lesions on stem
			25	0	
			23	0	
			22	3	1 with several old lesions, 2 with new lesions, apparently secondary infection
			25	2	2 with one new lesion, apparently secondary infection
			25	0	
		2 checks, not inoculated	25	1	1 old lesions
			25	0	
			25	0	
		4 recently inoculated	24	24	Stems badly affected
			22	22	Ditto
			22	19	Ditto
			24	17	Ditto

April 13 may not have given infected plants because the surface of the soil had been allowed to remain dry for some time through neglect. As no new spores had been produced to vitiate the experiment, these pots were replanted on May 7.

It would appear from this experiment that a few spores are able to live over winter in the soil outdoors and bring about infection the following spring. It is but fair to say, however, that the plants were not in any case screened from greenhouse insects that were present, and that other inoculation experiments with bean anthracnose were being conducted by other persons in another compartment of the same house and in adjoining houses. This may account for the few cases of disease occurring in the spring experiments. The infection is very light compared with that occurring on plants grown in freshly inoculated soil. Under practical bean-growing conditions the chances of infection from this source must be negligible.

An experiment similar to the one recorded above was tried the following winter, the same methods being employed. A greater effort was made, however, to keep the surface of the soil moist at all times, and also unsterilized but presumably uncontaminated soil, as well as sterilized soil, was used. On January 5, 1918, all the pots were well moistened with tap water, soon after which a suspension of spores was poured over the

surface of the soil of those to be inoculated. Sterilized sphagnum was then placed over the soil to the depth of an inch, and covers were tied over the tops of the pots. After three days some of the pots were placed outdoors, being set in the soil so that the tops were level with the surface of the ground; others were left inside the violet house, where the temperature is kept cool. Check pots not inoculated were similarly prepared. At each planting made thereafter a control pot, made up of fresh uncontaminated soil, was inoculated in the same manner as were the pots inoculated earlier. Twenty-five clean beans of the variety Refugee Wax were planted in each pot except in the first planting, when the variety Extra Early Refugee was used. After planting, the pots were kept in the warm house. The results are given in table 4.

TABLE 4. RESULTS OBTAINED BY PLANTING BEANS AT VARIOUS TIMES IN SOIL INOCULATED WITH A SUSPENSION OF SPORES OF COLLETOTRICHUM LINDEMUTHIANUM, AS COMPARED WITH THOSE GROWN IN UNINOCULATED SOIL

Date of planting	Date of examination	Description of pots used	Number of plants appearing	Number of plants affected	Remarks
Jan 5, 1918	Jan 25, 1918	Check (not inoculated):			
		Soil sterilized	25	0	
		Inoculated			
		Soil not sterilized	22	21	Varying from 2 excellent, to those with a slight lesion at base of stem
Jan 17	Feb 17	Check (not inoculated):			
		Pots left outside			
		Soil sterilized	17	0	
		Inoculated			
		Pots left outside.			
		Soil sterilized	21	1	Slight lesion on stem
		Soil not sterilized..	7	0	
		Pots left inside			
		Soil sterilized	23	2	Fair halfway up stem
		Soil not sterilized .	17	5	One or more lesions on stem
Feb 20	March 11	Check (not inoculated).			
		Pots left outside			
		Soil sterilized	21	0	
		Soil not sterilized.	13	0	
		Inoculated			
		Pots left outside			
		Soil sterilized	20	0	
		Soil not sterilized .	15	0	
		Pots left inside			
		Soil sterilized	20	0	
		Control (fresh soil used):			
		Soil inoculated 2 20–18.	19	19	Lesions, many of them large, on stems

TABLE 4 (*continued*)

Date of planting	Date of examination	Description of pots used	Number of plants appearing	Number of plants affected	Remarks
April 3	April 19	Checks (not inoculated):			
		Pots left outside:			
		Soil sterilized	24	0	
		Soil sterilized	18	0	
		Inoculated			
		Pots left outside			
		Soil sterilized	22	0	
		Soil sterilized	19	0	
		Soil sterilized	19	0	
		Soil not sterilized..	25	0	
		Soil not sterilized.	18	0	
		Pots left inside:			
		Soil sterilized	24	0	
		Soil sterilized	19	0	
		Soil not sterilized	13	0	
		Control (fresh soil used):			
		Soil inoculated 4-3-18	16	13	Excellent on stems

It appears fairly evident that spores of *C. lindemuthianum* removed from the acervulus and remaining in the soil for a period of two weeks or more are able to bring about an infection of susceptible bean seedlings grown in such soil, but not after six and one-half weeks. Under field conditions, however, in addition to spores being washed into the soil, there are many bits of plant tissue, some of which would probably be infected tissue, remaining on the soil after the beans are harvested.

Frank (1883 b:521) tested the germination of spores which he found produced in the lesions of dry seed. He concludes that spores attached to the basidium remain viable throughout the winter, while those produced earlier and unattached are unable to survive. Edgerton (1910:20) has studied in a different way the question of the viability of these spores. He finds that the old spores on or within affected seeds are capable of germinating in nutrient media, and suggests the possibility of the infection of seedlings from healthy seeds by such spores, they having been transferred to the healthy seed by contact with affected ones. He finds also that good germination takes place in agar after the spores have remained dried for thirteen days in their mucilaginous matrix or washed free from it, and states that some germination took place after twenty-two days had elapsed.

Infection was also brought about, in an experiment, by placing recently affected vines or pods on or in the soil before the bean plants appeared. On August 8, 1910, vines of the current year badly affected with anthracnose were placed in a flat and covered to the depth of an inch with soil. On the surface of this soil, fifty hand-sorted Refugee Wax bean seeds were planted. These were covered lightly with soil. The soil came from a neighboring field that had not produced beans for years. The flat was then placed outdoors and watered once with well water. All the seeds produced plants, which on August 22 were not affected on any part above ground. On August 29 forty-two plants had appeared, of which thirty-five, or 83⅓ per cent, showed lesions on stem, on leaves, or on both.

On August 22 one hundred clean Refugee Wax seeds were planted in clean soil in a flat and covered lightly with soil. Over the surface was placed a quantity of immature pods badly spotted with anthracnose and producing spores. On September 6 ninety-eight plants had appeared, of which ninety-four, or 95.9 per cent, were infected.

Halsted (1896.286) has shown how beans planted in ground on which diseased plants were grown the year before, gave from four to six times as many spotted pods as did beans grown on new land; he found also (1896 288 and 1897:330) that mulching the soil with diseased pods from the preceding season caused an increase in the number of spotted pods over those in soil mulched with hay. This would lead to the belief that the fungus is capable of living over winter as spores in the soil or as spores or mycelium in the diseased pods.

Observations were made each year from 1910 to 1914 to determine whether soil which the preceding year had produced plants badly affected with anthracnose could serve as a source of inoculum to seedlings. Healthy seed planted in such soil gave in every instance seedlings that were free from anthracnose and remained so for a considerable time afterward.

Tests were made to determine whether the fungus can live over winter in old pods and vines. Badly spotted pods stored in paper sacks in an attic were found during the late winter and early spring to possess a thin black mycelial growth over their surface outside of the old lesions, and scattered thickly in places on this growth were small black bodies

resembling pycnidia as viewed with a hand lens (fig. 14). A section through these bodies examined under the microscope showed them to be compact

FIG. 11. SAPROPHYTIC DEVELOPMENT OF ANTHRACNOSE ON SURFACE OF DRY PODS

acervuli containing a large number of setae. The conidia, present in large numbers, germinated readily in a nutrient solution, and when healthy plants were inoculated with them anthracnose lesions appeared. The

growth seems to be of a saprophytic nature, as the pods were dry when picked and at that time none of this growth was observed. Other isolations of *C. lindemuthianum* have been made from dry bean pods from time to time, even from pods more than a year old.

Trials were made also to determine whether old pods and vines affected by anthracnose may serve as a source of inoculum to seedlings. In the fall of 1911 a plot of ground where anthracnose had appeared to a severe extent on beans was selected for experiment. The diseased vines were left there, and diseased vines from other places were spread on the plot, all being plowed under the following spring. On June 13 a short row of each of five varieties was planted with seed from selected healthy pods. Adjoining these, one row of each of two varieties was planted with seed spotted with anthracnose. The seedlings were appearing on June 19. In several examinations made before June 25, the plants from the healthy seed showed no affection with anthracnose, while the young leaves of the plants from spotted seed were severely affected. Eight plants from healthy seed were found to be affected on July 1 as shown in table 5. This may have been due to secondary infection. The order in which the varieties appear in the table is the order in which they were planted in the plot.

TABLE 5. RESULTS OF AN EXPERIMENT TO DETERMINE WHETHER OLD PODS AND VINES AFFECTED WITH ANTHRACNOSE CAN SERVE AS A SOURCE OF INOCULUM TO SEEDLINGS

(Seed planted on June 13, 1912; data taken on July 1, 1912)

	Varieties planted with healthy seed					Varieties planted with seed spotted with anthracnose	
	Blue Pod Medium	Turtle Soup	California Cream	Navy Pea	Red Marrow	Navy Pea	Red Marrow
Number of plants appearing	306	492	346	1,070	1,473	198	262
Number affected with anthracnose	0	0	1	2	5	81	95
Per cent affected with anthracnose	0	0	0.3	0.2	0.3	41	36

While observations were made each year as to the possibility of infection of seedlings from overwintered vines, no further definite efforts were made to determine this point until the fall of 1915, when a series of experiments

was planned with this end in view. In these experiments the beans were planted in soil in ordinary greenhouse flats. Each flat was numbered, and the conditions involved in the case of each are given herewith. Seeds from healthy pods were used for planting each flat except flat 2, for which seeds spotted with anthracnose were used.

Flat	Description
1	Clean soil
2	Clean soil. Seeds spotted with anthracnose used in planting
3	Contaminated soil
4	Contaminated soil sifted to remove particles of bean tissue
5	Clean soil. Diseased vines and pods from crop of 1915 obtained from disease garden, broken up and mixed with soil in flat
6	Clean soil. Diseased vines and pods from crop of 1915 obtained from disease garden, placed on surface of soil and removed as seedlings were appearing
7	Clean soil. Diseased vines and pods from crop of 1915 obtained from disease garden, placed on surface of soil and left there
8	Clean soil. Diseased vines and pods from crop of 1915 kept in seed house, placed on surface of soil and left there
9	Clean soil. Diseased pods from crop of 1916 kept in seed house, placed on surface of soil and left there

The clean soil (uncontaminated by *C. lindemuthianum*) used was taken from a field where no beans had ever been grown so far as was known, but it was not sterilized except in the last experiment, when it was thought to be contaminated with spores. The flats, unless new, were sterilized with steam. The contaminated soil came from places in the disease garden where bean plants badly affected with anthracnose had grown in 1915. Only the surface soil to a depth of from two to four inches was used. In the first experiment both sifted and unsifted soil was used, but thereafter all contaminated soil was passed through a rather fine sieve in order to remove particles of bean-plant tissue as far as possible.

The healthy seed used was selected from clean pods, and in all but two experiments (II and III) it was immersed for three minutes in a 1 1000 mercuric chloride solution and afterward washed in tap water. This was done to destroy any spores of *C. lindemuthianum* that might possibly be present. The affected seed was disinfected in the same way as was the healthy seed. Seed so badly diseased that it could not germinate was not used. The affected seed used in each experiment was of the same

variety as the healthy seed used. Davis White Wax was used in all experiments except Experiment IV, in which Refugee Wax was used. The old vines and pods affected by anthracnose were of several varieties and no attempt was made to keep them separate. Most of them were well covered with anthracnose lesions. Care was taken to remove all seeds, even shriveled ones, from the pods. The vines and the pods left in the garden over winter were much overrun with numerous saprophytic fungi and were somewhat decomposed by spring. Those kept in the seed house were as intact as they were when placed there.

In setting up an experiment, for example flat 6, the soil was first placed in the flat, the seed was then disinfected and planted usually in four or five rows to a flat, the vines and pods were placed over the surface to a depth of about one and one-half or two inches, the flat was placed in the greenhouse, and tap water was sprinkled on it until the soil was saturated. Unused sphagnum was placed over the flats unmulched by pods or vines in the case of Experiments V and VI. Each flat was prepared separately and every precaution was taken to avoid contaminating one with another.

The temperatures at which the flats were kept in the different experiments varied considerably, but when possible they were kept between 65° and 70° F. This was done in order to favor the fungus and permit infection to take place, and for this reason also the flats were watered more profusely than is best for good germination of bean seed. As a result the germination was very poor in some instances.

Records giving the extent of affection are not included here as they are all very much alike. On nearly every plant the stem was affected with one or more lesions, and often these occurred only at the surface of the ground. A few plants had lesions on the leaves. Lesions on cotyledons coming from the spotted seed used in flat 2 were not considered. The records were usually taken in about three weeks or less after the experiment was set up, in order to get them before secondary infection occurred. There is no doubt that secondary infection did occasionally occur.

These experiments, the results of which are shown in table 6, cannot be regarded as ideal. The results obtained in some cases — for example, from flat 1 in Experiment II — may seem to cast doubt on their reliability. But when the entire series is considered, there can be no doubt that the results show the possibility that old bean pods and vines serve as a source

TABLE 6. RESULTS OF A SERIES OF EXPERIMEN S TO DETERMINE WHETHER CONTAMINATED SOIL OR ANTHRACNOSE-AFFECTED VINES AND PODS OF VARIOUS AGES CAN SERVE AS A SOURCE OF INOCULUM TO BEAN SEEDLINGS

Experiment, and date when set	Flat	Number of plants appearing	Plants affected	
			Number	Per cent
I Nov. 24, 1915	1	12	0	0
	2	47	12	26
	3	24	0	0
	4	35	16	46
	5	24	19	79
	6	17	15	88
	7	14	14	100
II Dec. 29, 1915	1	44	11	25
	2	26	16	62
	4	45	0	0
	5	47	31	66
	6	24	21	88
	7	48	28	58
III April 28, 1916	1	35	0	0
	2	33	16	48
	4	41	0	0
	5	32	2	6
	6	25	5	20
	7	30	4	13
	8	18	15	83
IV June 7, 1916	1	38	0	0
	2	22	21	95
	4	37	0	0
	5	40	2	5
	6	39	1	3
	7	39	35	90
	8	38	34	89
V Nov. 10, 1916	1	34	0	0
	2	26	22	85
	8	31	31	100
	9	38	38	100
VI June 13, 1917	1	8	0	0
	2	17	9	53
	8	12	6	50
	9	72	34	47

of inoculum for the infection of bean seedlings. Apparently soil that is devoid of affected bean tissue cannot serve as a source of inoculum for more than two or three months, or is not an important factor in bringing about infection even though a few spores may live over winter in it.

In order to determine whether old affected vines and pods can serve as a source of inoculum under conditions prevailing out of doors at planting time in the spring, Davis White Wax beans were planted on June 10, 1916, in clean soil in the disease garden; that is to say, in soil in which beans had not been grown since 1911, at which time they were badly affected with anthracnose. Four rows, with forty hills to a row and five seeds to a hill, were planted in the following manner and with the following results (recorded June 26):

Row 1. Seed spotted with anthracnose planted. No mulch used. Only fifteen plants in six hills were alive, all of which showed affection with anthracnose.

Row 2. Clean seed planted, and hills mulched by placing over each a handful of old affected vines left outdoors in a pile over winter. One hundred and sixty-five plants appeared, every one affected on stem or leaves or both.

Row 3. Clean seed planted, and hills mulched by placing over each a handful of old affected vines kept dry in seed house. One hundred and seventy-one plants appeared, every one affected on stem or leaves or both.

Row 4. Clean seed planted. No mulch used. This row was about a rod north of the others. One hundred and sixty-nine plants appeared, on which no infection was observed at this time.

The weather from June 10 to June 15 was clear and warm most of the time and was favorable for seed germination. From the evening of June 15 to June 21 inclusive it was cool and rainy or cloudy, weather very favorable for infection to take place. From June 22 to June 26 inclusive it was clear and warm.

These results plainly indicate that under favorable conditions in the field, affected bean pods and vines from the crop of two preceding years can serve as a source of inoculum when they come into contact with seedlings of a susceptible variety of beans. Nevertheless it is probable that but little infection takes place from contaminated soil or from overwintered vines that are plowed under in preparing the land. In these experiments special pains were taken to place a considerable amount of badly affected

bean tissue where it would be in continued contact with the seedlings. In ordinary practice this would occur only accidentally if at all. But when considerable wet weather follows planting, infection may be expected to occur from contact with old affected vines spread with manure on the surface of the soil after plowing, or from such affected vines as come to the surface after having been plowed under.

Muncie (1917:15–21) carried on tests to determine whether the bean-anthracnose and bean-blight organisms are able to winter over in old bean trash containing affected vines or as spores in the soil. He observed during the summer a small amount of anthracnose on the plants grown in pots where spores had overwintered and where old anthracnose-spotted vines of the second as well as the next preceding year had overwintered. A greater number of plants became affected with blight in these trials. From these data Muncie is convinced that the causal organism of both anthracnose and blight can live over winter in the soil in diseased bean trash and as spores or bacteria in the soil, and infect the crop of the following season. His field observations of preceding years doubtless strengthen this opinion.

Schaffnit (1920) obtained spores with unimpaired germination up to February 12, 1920, from pods of the harvest of the preceding year. Meyer (1910) finds the first appearance of the disease always on plants growing on damp ground directly where fresh stable manure has been applied but not where commercial fertilizers have been used. Pfeiffer (1910), however, believes the organism does not come from manure, as he has observed the disease commonly on land that never receives it. Muncie (1917:21) records inoculations made with an inoculum consisting of dung from a cow fed with bean straw infected by *C. lindemuthianum* and *Bacterium phaseoli*, but states that he was unable in this way to produce anthracnose and that blight appeared on only one plant. It is not unlikely that beans planted on heavily manured ground would produce so rank a growth that moisture conditions about them would be more favorable for infection than with plants not so vigorous. It is also possible for the pathogene to be introduced into a field with manure having infected bean straw mixed with it.

Further infection of the plant and spread of the disease through the field

The inoculation of the leaves, the petioles, the branches, and the inflorescence of the older plants occurs in the same manner as that of

the seedlings. The plants, being larger, are more likely to be in contact with one another and thus make easier the transmission of the spores. If the vines have a tendency to hang low and be bushy, the air beneath them remains sufficiently humid for spore germination for a longer time after rains and dews than does the air outside. During rains the drops of water on the plant run together and move over the surface, in some places dripping from the leaf apices to other leaves and vines, in other places running down the stem or falling in large drops on the pods, where they spread out over the surface as they strike. When wind accompanies a storm, the wet leaves are blown against one another, against the leaves and stems of other plants, or to the ground. If a plant is affected with anthracnose, multitudinous spores from the various lesions become suspended in the rain water and are carried as described to the healthy parts of the plant. The pods become inoculated in this manner and in other ways.

When falling raindrops strike a spore-producing lesion or a film of water anywhere containing spores, drops of the contaminated water are spattered to the near-by stems and leaves. Faulwetter (1917), in his efforts to explain the rapid dissemination of *Bacterium malvacearum*, has made some interesting experiments to determine the distance to which water can be splashed by falling drops of various sizes. He finds that splashing occurs only when drops fall on a film of water, and that it is the water of the film that is splashed. A drop 0.1 cubic centimeter in volume falling 16 feet onto a film over a glass plate spattered water as far as 64 inches. A drop 0.02 cubic centimeter in volume falling 16 feet during a wind of 10 miles an hour "splashed water in abundance a distance of 8 feet..... in moderate quantities as far as 12 feet..... and in slight amounts to 16 feet." He concludes that the possibilities of dissemination of bacteria in suspension in film water on cotton leaves are considerable if one includes the distance bacteria may be carried from the original lesion, then splashed up again and carried farther, and so on, until a dilution too great for infection is obtained."

In addition to being splashed from contact with falling raindrops, contaminated drops of water may be carried bodily during a heavy wind to healthy parts of the plant, and plants blowing against one another will aid in disseminating the spores. Persons, as well as dogs, rabbits,

pheasants, and other animals, passing through the field when the plants are wet, may serve to carry the spores from one plant to another. Insects, although minor agents, no doubt aid in inoculating healthy plants.

Gardner (1918:34) has shown conclusively that after a rain the spores of *Colletotrichum lagenarium* are present in the soil beneath affected plants, and that they may be disseminated by the spattering of such soil during a rainstorm. He has shown also that spores may be carried across a field in surface water during storms and washed or spattered onto healthy plants, infecting them and thus greatly enlarging the foci of infection.

No field observations of the spread of the bean-anthracnose disease were made during the three years when the writer's field work was done, since the disease appeared to only a slight extent during that time. What has been said regarding the spattering of contaminated water and soil in the dissemination of the two diseases mentioned would seem to be true in the case of *C. lindemuthianum*. Certainly the similarity of this organism and *C. lagenarium* in the matters of spore production, character of spores, and method of infection, would lead to the conclusion that the means of dissemination and inoculation shown in the case of the cucumber-anthracnose organism would exist also in the case of the bean-anthracnose fungus.

Infection of seeds

The appearance and extent of the canker on the seed, and its progress from pod to seed, are described on pages 107 and 111. As the pod matures, the seeds within prepare for a resting period. The cells, now packed with reserve food, become denser, drier, and more capable of resisting decay. The mycelium of the fungus within the cells of the seed also becomes less active, and possibly entirely dormant. It renews its growth, however, at conditions of temperature and humidity to which the embryo of the seed responds but slowly. There is probably very little activity of the fungus in seed stored in a dry place. Halsted (1892:285) and others report having found viable spores on and within spotted seed stored in such a place, and the writer has often so found them. The acervuli were black and dry, and it was not ascertained whether spores were being produced under such conditions or whether they were produced earlier

when the seed was in a more moist condition. Just how long the fungus can live in old seeds has not been determined, although cultures were obtained from seeds two years old.

Infection studies

Susceptibility of plants of different ages to infection

But little evidence has been presented by investigators concerning the susceptibility of plants of different ages to infection. Frank (1883 a: 34) and others find that young and half-grown pods are more susceptible than older ones. Edgerton (1908: 397) remarks that the young bean plant is not readily infected, but his later work (1910: 41) indicates that he had but little trouble in securing infection on seedlings. Cook and Taubenhaus (1912: 49), noting a correlation in this first statement of Edgerton's with results which they had obtained on young fruits of apple and pear with several Gloeosporia attributed by them to the presence of an enzyme capable of forming a tannin-like body toxic to fungi, tested the oxidizing power of the enzyme present in the bean plant at various stages of its development and found that the oxidizing power is greatest in the young bean plant, is small during blossoming and the formation of young pods, is large again when the plants have large green pods, and decreases again when the pods are yellow. After making numerous inoculations on plants at all stages of growth, the writer is convinced that a young bean plant is more susceptible than an older one, and that young parts are more susceptible than older parts. An experiment was made in 1910 in which Refugee Wax beans were planted at intervals of seven and eight days throughout the season, beginning on June 27 and ending on August 22. In the evening of August 31, three days after the beans last planted appeared, all plantings were inoculated by spraying a suspension of spores over all parts of the plants. During the following day the plants were protected as far as possible from drying out by placing wooden boxes over the hills. When observed six days later, all the seedlings were badly infected and some were dying. Good infection was obtained on the younger leaves and petioles of beans planted one month earlier, but slight infection on the older leaves. Those planted two months earlier and having some mature pods were only slightly affected on leaves and vines, but good infection was obtained on young pods. The nearly mature pods showed no evidence of infection. The writer has always obtained

good infection on pods of susceptible varieties when inoculated under favorable conditions for infection before they passed their brittle, or "snap," condition.

Susceptibility of different parts of the plant to infection

As mentioned in the preceding paragraph, Frank (1883 a) says that young bean pods are more subject to attack than are older pods, and this has been noted also by other early writers. Frank further found the pods to be more susceptible than the stems, the leaves, and the petioles, although inoculation on young bush beans resulted in the appearance of lesions on the hypocotyl, the epicotyl, and the veins of young leaves. He found the cotyledons especially susceptible. Scribner (1888) states that parts of the plant other than the pods and the seeds are rarely attacked. Edgerton (1910:42) found that when bean seeds were inoculated with spores of the fig- and the cotton-anthracnose fungi, these organisms were able to attack and grow in the semi-living cotyledons but did not infect other parts of the plants. However, the cotyledons are to be regarded rather as culture media than as host tissue. Lauritzen (1919:33) says the secondary leaves of the bean are more pubescent and seem to be affected more easily at the limiting humidities. This seems to be due to favorable humidity rather than to susceptibility. Others, in writing on the subject, have usually described the disease as occurring on the leaves, the stems, the pods, the seeds, and the cotyledons. The writer has found all young parts of the plant, including the roots, subject to attack, but as they become older they grow more resistant. The tissues of the seedling and of the young pod appear to be the most susceptible. The epicotyl of young bean plants of varieties showing marked resistance to the disease has often become affected when the plant was inoculated, although the other parts showed no lesions. In such cases, resistance may be due to the inability of the infection tube to penetrate the cuticle.

Susceptibility of different varieties of Phaseolus vulgaris L. to infection

In a number of the treatises on bean anthracnose, certain varieties are mentioned as being more susceptible to the disease than other varieties, but in most cases no inoculation experiments have been conducted to confirm these statements. Frank (1883b:511) says that Lindemuth observed the disease on the red-mottled Zucker-Stangenbohnen while other

varieties near by were not affected, but a few years later he found many varieties susceptible. Trelease (1885), in speaking of the "peculiar susceptibility of the white-podded bean," says that "it is not improbably connected with the delicacy of its tissues, which selection has produced." Scribner (1888) states that wax, or butter, beans — those having yellow pods — are the kind most subject to attack, and later (1889) finds that no variety is exempt, not even those with green pods. McCarthy (1892: 14) says that wax varieties are especially susceptible. Harvey (1894) finds the disease worse on white-podded bush and pole beans. Cobb (1894:379) says that all varieties of *Phaseolus vulgaris* are attacked, though the tenderness of the wax (or butter) beans makes them more susceptible. Halsted (1898:312), after growing six varieties of beans, finds Green Flageolet the most susceptible to anthracnose and blight. Whetzel (1906) states that probably all the "rust-proof" varieties placed on the market will spot under conditions most favorable to the fungus. Tracy (1907), in his notes on varieties, records considerable variation in their susceptibility to anthracnose. Jarvis (1908:162) finds that, while wax-podded varieties are more susceptible, some desirable green-podded beans also are affected. Edgerton (1910:49) finds a number of wax varieties with which he has been working to be very susceptible. He finds Valentine somewhat resistant, and Nox All highly resistant on leaves and stems; and he speaks of Hodson Wax as having a reputation among growers for resistance, although he finds it somewhat susceptible. He thinks that observations of the amount of anthracnose on different varieties growing side by side is of little value in determining their resistance, and believes that the only way to test their resistance in a satisfactory manner is to inoculate each variety with the spores of the fungus. Ferraris (1913) lists a few very susceptible and a few resistant Italian varieties.

The writer (Barrus, 1911) has inoculated a large number of varieties of *Phaseolus vulgaris*. At the time when that work was done, no variety tried proved entirely immune to all cultures. However, it was discovered that there are at least two forms or strains of the organism physiologically different from each other although morphologically and culturally alike. Certain varieties of beans resistant to one of the strains were susceptible to the other, and those resistant to the latter strain were often susceptible to the former. There were other varieties that

were susceptible to all strains, but none were found that were resistant to all. Edgerton and Moreland (1916) inoculated twelve varieties of *P. vulgaris* with cultures of the pathogene from eleven sources and obtained somewhat similar results. The snap varieties generally were susceptible to all cultures, while the Scarlet Runner and a variety which these authors call "Large White Kidney" were resistant to all. Three distinct types of cultures were found among those tried: one able to infect all varieties except the two mentioned; a second that affected the Boston Pea and snap beans but was not able to affect the Red Kidney to any extent; and a third that brought severe infection to the Red Kidney, moderate infection to the snap beans, but only slight infection to the Boston Pea. Fischer (1919:254) records the observations of several German writers concerning the comparative resistance of the different varieties grown in Germany. Some are inclined to think that the wax varieties are more susceptible, others that green snap beans are. Several have observed that pole varieties are more resistant than bush beans, but Fischer says the greater freedom of the former from anthracnose is due to their position on poles, where the conditions are not so favorable for infection as with vines near the ground. He is inclined to believe that the contradictory observations show the existence of different strains of the organism in the various localities. These observations, and those made by him on twenty varieties planted so as to become infected from spotted seed planted among them, lead him to believe that there is no variety in Germany resistant to anthracnose at all times and under all conditions. The most resistant variety of all appears to be Ideal Wachs-Buschbohne. Schaffnit (1920) observed the relative degree of infection on forty-five varieties of beans during 1914 and 1915 at six different localities in Germany, and lists a number of German varieties under each of the following headings: least attacked, moderately attacked, badly attacked. In general he found that varieties descended from the stem "Flageolet" are the most affected, while those descended from Hinrichs Riesen are the least affected; also, that pole beans show much greater resistance than do bush beans. This suggested to him the possibility of crossing pole and bush beans in order to obtain a resistant bush variety. This work he had not completed at the time when he prepared his paper.

The writer (Barrus, 1918) reports the results of a large number of inoculations made on many varieties of *P. vulgaris* and of other beans,

with cultures from fifteen different sources. These for the most part fell into two physiological forms or strains, which are designated, respectively, as *alpha* and *beta*. The varieties of beans, from their behavior when inoculated with these strains, showed a classification into four groups, as follows: ab, those susceptible to either strain of the pathogene; Ab, those resistant to *alpha* but susceptible to *beta*; aB, those susceptible to *alpha* but resistant to *beta*; and AB, those showing resistance to both *alpha* and *beta*. In the first-named group, ab, belong 80 per cent of the wax bush varieties inoculated, 50 per cent of the green-pod bush, 40 per cent of the wax pole beans, and 30 per cent of the green-pod pole beans. It appears from this, then, that the wax bush beans are, generally speaking, the most susceptible to anthracnose. Five varieties are placed in the resistant group AB, but of these only one, Wells' Red Kidney, has shown a satisfactory resistance under all conditions. The writer (Barrus, 1915) described this strain of Red Kidney as having been selected by a farmer as a single healthy individual from a field where all other Red Kidneys were badly affected. This strain has continued to show the same resistance in the many inoculations made by the writer and by other investigators. It is not a pure type, however, the seed varying somewhat in size, shape, and color, and individuals appear from time to time which show some susceptibility to anthracnose, varying from slight to considerable. In a later paper (1918:602) the writer records the resistance of a field bean called White Imperial to several inoculations made with both strains of the pathogene. Recently, however (in 1921), a field of beans said to be White Imperial, the pods of which were severely affected with anthracnose, was observed. It seems not unlikely that strains of the pathogene exist which are capable of infecting even these varieties.

Burkholder (1918:353) has been able to produce an anthracnose-resistant White Marrow by crossing the ordinary susceptible White Marrow with the resistant Wells' Red Kidney and by subsequent selection of the resistant types. In the same manner, McRostie (1919:141) has also reported crossing the Wells' Red Kidney with the Michigan Robust, a white pea bean, but progress had not been made beyond the F_2 generation at the time of this report. In both of these crosses the character of resistance proved to be dominant, and inoculation of the F_3 generation is necessary in order to determine which individuals are homozygous and which are heterozygous to resistance.

No continued efforts have been made, so far as the writer is aware, to render susceptible bean plants immune to anthracnose by the absorption of toxic substances, as has been attempted with some other plants. The writer has endeavored to obtain a greater degree of susceptibility in bean plants showing considerable resistance to one of the strains of *Colletotrichum lindemuthianum*. Such plants, while yet seedlings, were, just previous to inoculation, (a) kept growing in very dry soil for two weeks, (b) kept in very wet soil for two weeks, (c) injured in various ways. In no case was a greater degree of infection obtained than on plants not so treated. Schaffnit (1920) remarks that a weak condition of plants such as comes from a sudden check in growth, as during a sudden fall in temperature, makes them especially susceptible.

Susceptibility of other species of the genus Phaseolus to infection

The statement has sometimes been made that varieties of *Phaseolus vulgaris* only are susceptible to attack by *Colletotrichum lindemuthianum*. Massee (1898), however, reports the disease as most common on French beans (*Phaseolus vulgaris*) and on Scarlet Runner (*P. multiflorus*), and a few other writers on the subject have recorded it as being severe or as occurring on Scarlet Runner (*P. multiflorus*), possibly quoting from Massee (Saccardo 1898, Collinge 1911, Lind 1913). Allescher and Schnabl (1893) distributed specimens of *Gloeosporium lindemuthianum* on leaves of *Phaseolus multiflorus*. Lakon (1916) says that *P. multiflorus* is practically resistant to rust and above all to anthracnose. Schenk (1917) also says that, although the disease is reported as occurring on Feuerbohnen (*P. multiflorus*) in Holland, he has observed this species to be very resistant when other varieties were badly affected. Fischer (1919:258) saw nothing of the disease worth mentioning on three varieties of *P. multiflorus* — *albiflorus* Lam., *coccineus* Lam., and *bicolor* Arrabida — while pole beans of *P. vulgaris* growing next to them were badly affected. Edgerton (1910:41) reports a slight infection of lima beans (*Phaseolus lunatus* var. Small White Pole), and later (with Moreland, 1916:8) good infection on Fordhook's Bush Lima, very slight infection on Large White Kidney, and no infection on Scarlet Runner when inoculated with spores of *Colletotrichum lindemuthianum*. Lind (1913) records the disease on pods, stems, and leaves of *Phaseolus vulgaris*, *P. compressus*, *P. nanus*, and *P. multiflorus*. The

ecific name *nanus*, however, refers to the bush forms of *P. vulgaris*, d the name *compressus* to another classification of varieties now included *P. vulgaris*.

The writer has reported (Barrus, 1918:610) some good infections from oculations made at various times during several years on the leaves of number of varieties, both pole and dwarf, of *Phaseolus lunatus* L., both e small, or sieva, lima and the large lima. Fair infections were obtained the stems, and also, from field inoculations, fair to good infections on e pods (fig. 15). From inoculations made at various times, the varieties arlet Runner and White Dutch Runner, of *P. multiflorus* Willd., have own slight to fair infection on leaves and pods; the latter variety especially owed fair infections on pods (fig. 16) and seeds. The tepary bean, *acutifolius* var. *latifolius* G. F. Freeman, has always become badly fected when inoculated in the seedling stage.

The article just cited reports also the results of inoculations made on m one to several varieties of a number of species of Phaseolus supplied E. V. Piper, of the United States Department of Agriculture. Slight fection was obtained on *Phaseolus aureus* Roxb., but on *P. aconitifolius* eq., *P. angularis* (Willd.) W. F. Wight, *P. calcaratus* Roxb., *P. mungo* , *P. semierectus* L., and *P. sublobatus*, no definite infection resulted.

Susceptibility of plants of other genera and families to infection

Frank (1883 b:518) obtained no infection on cucumbers which he inoculated with anthracnose. Scribner (1888:362) states that the fungus tacks watermelon rinds as well as beans. Farlow and Seymour (1888) d Saccardo (1898:316) record it as occurring on *Citrullus vulgaris* Schrad. dloway (1889) ascribes the disease "melon rust" to *Gloeosporium demuthianum* Sacc. & Magn. Halsted (1893 b:327, 329) obtained fection, from beans, on detached fruits of eggplant, pear, citron, pepper, d persimmon, and he believes (page 333 of reference cited) that the three lanaceous plants, tomato, eggplant, and pepper, are preyed upon by e same *Colletotrichum lindemuthianum* which causes a pod spot of the an. Stoneman (1898:93) points out that inoculations made on detached uits placed under a bell jar cannot be depended on, as such fruits are uch less resistant to attack than are fruits under normal conditions, d are more in the nature of culture media. Smith (1904:28) obtained ul infection from inoculations made on bean, but none on cucumber,

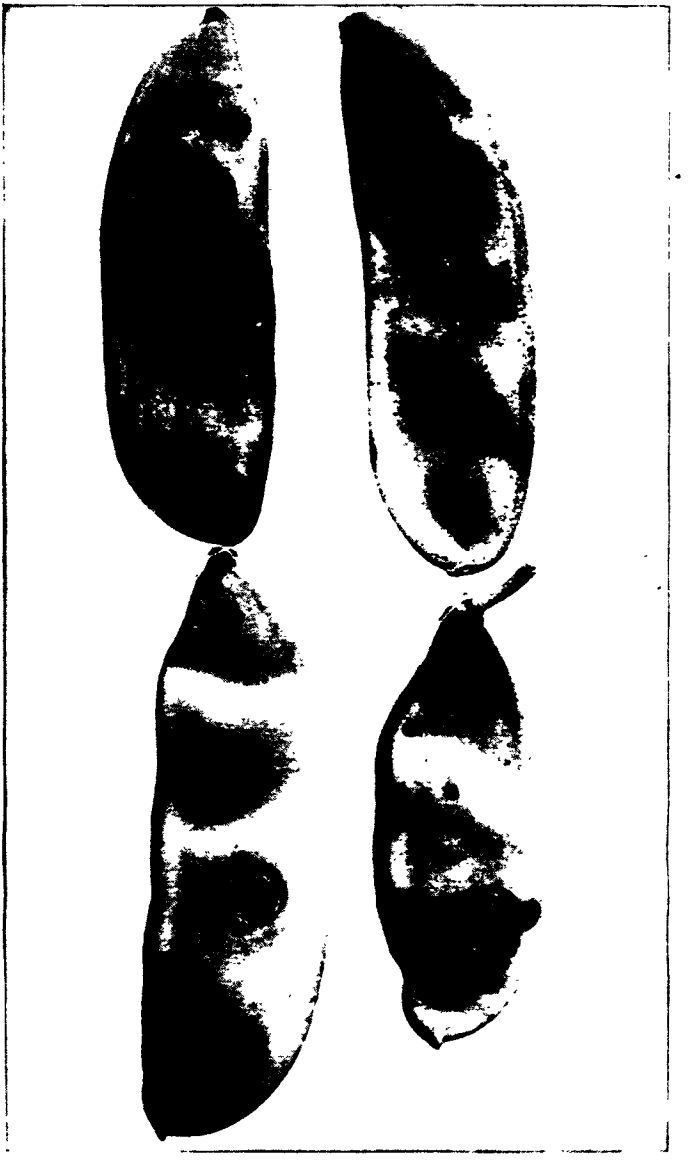

FIG. 15. ANTHRACNOSE ON PODS OF PHASEOLUS LUNATUS, LIMA BEAN

pumpkin, squash, watermelon, and muskmelon. Cook and Taubenhaus (1912 22, 27) obtained only negative results from inoculations of young

FIG. 16. ANTHRACNOSE ON PODS OF PHASEOLUS MULTIFLORUS VAR. WHITE DUTCH RUNNER, PRODUCED BY ARTIFICIAL INOCULATION MADE ONE MONTH BEFORE PHOTOGRAPH WAS TAKEN

ripe apples and pears with *C. lindemuthianum*. Edgerton (1911:8) so was unable to infect apples with this organism from inoculations

which he made on picked fruit kept in a moist chamber. He was unsuccessful also in his attempts to infect the leaves, stems, and fruit of cucumbers with this fungus (Edgerton, 1910:41). Shear and Wood (1913:78) inoculated fruit of apple, young wax bean pods, young cotton bolls, a mature pumpkin, a mature squash, green tomato fruits, and a nearly mature watermelon, with the conidia of the bean-anthracnose fungus, punctures being made in all except the bean pod, in which case the spores were applied to the surface; but in no case, not even with the beans, was infection obtained. It is possible that the beans inoculated were resistant to the strain of the pathogene employed. Krüger (1913:294) inoculated beans and cucumber fruits kept under the same bell jar, getting good infection on the beans but none on the cucumber even when it was injured, and he concludes from this that the forms occurring on the two plants are different. Inoculations which he made on apples, bananas, and tomatoes were unsuccessful on the first two, although they resulted in a whitened, sunken, spore-producing area about the punctures.

Chester (1894) reports that many seedlings of cowpea (*Vigna sinensis* Endl.) of the Conch variety died as a result of an attack of anthracnose caused by *Colletotrichum lindemuthianum*, and an examination of the seed showed that 9.5 per cent were diseased. McCarthy (1894:151) reports that pods of cowpeas nearly full-grown were occasionally attacked by a species of Gloeosporium. Butler (1918:262) reports an anthracnose on cowpea in India, saying that in general its characters agree with that of the bean but that experimental work is necessary before the two diseases can be pronounced identical. He records also (page 267 of reference cited) an anthracnose on val (*Dolichos lablab* L.) and on kulthi (*D. biflorus* L.) and tentatively refers the causal pathogene to *Glomerella lindemuthianum* (Sacc. & Magn.) Shear.

Sydow (1886) distributed what appear to be diseased pea pods (labeled *Vicia sativa*) under the name *Gloeosporium lindemuthianum*. Viala and Pacottet (1905) refer to *Colletotrichum lindemuthianum* as the fungus causing anthracnose of peas and beans, and Cooke (1906) reports it as being the cause of a disease of peas as well as of French beans. Other writers have not reported it on peas, and Edgerton (1910:41) could not secure infection from inoculations made on garden peas even after the wax was rubbed off the leaves. Fischer (1919:259) says that both Lemke and Feldt report having observed plants of *Vicia faba* severely attacked

by this fungus, but his own observations do not confirm this and he thinks the disease observed was due to some other fungus.

Edgerton (1910:40) also sprayed spores of *C. lindemuthianum* on young bush beans, alfalfa, and cotton plants protected by bell jars, but obtained infection on the beans alone. Bäumler (1888) reports *Gloeosporium lindemuthianum* as occurring on stems and leaves of *Orobus vernus*. It seems that in this case the species of the pathogene was incorrectly determined.

The writer, in the course of his infection studies with beans, has inoculated seedlings of sweet pea (*Lathyrus odoratus* L.) and garden pea (*Pisum sativum* L.), vines and young pods of cowpea (*Vigna sinensis* [L.] Endl.), and young plants of mandrake (*Podophyllum peltatum* L.), with spores of *Colletotrichum lindemuthianum*. Excellent infection was obtained on beans used as checks, but the other plants remained free from disease. In a series of other inoculation experiments on seedling plants, fair to good infection resulted on the stems of certain individual black-eyed beans or cowpeas (*Vigna sinensis* [L.] Endl.), and slight to fair infection on the epicotyl of the kulthi bean (*Dolichos biflorus* L.); but no infection resulted on any part of the bonavist bean (*Dolichos lablab* L.), the guar bean (*Cyamopsis tetragonoloba* Taub.), the asparagus bean (*Dolichos sesquipedalis* L.), the jack bean (*Canavalia ensiformis* [D.] DC.), four varieties of horse bean (*Vicia faba* L.), and the garbanzo bean, or chickpea (*Cicer arietinum* L.). There are evidently but few species outside the genus Phaseolus which are susceptible in any degree to anthracnose, and no plants except varieties of *Phaseolus vulgaris* are susceptible to such an extent that the disease becomes epiphytotic in regions where such plants are extensively grown. It is not unlikely that several strains of the pathogene exist, one capable of infecting *Phaseolus multiflorus* or some of its varieties in a severe manner, another able to attack *Vigna sinensis*, and others attacking plants related to the bean, each being confined rather closely to the species, or even to certain varieties within the species, to which they have adapted themselves.

Susceptibility of Phaseolus vulgaris to infection from other anthracnose fungi

Frank (1883 b:518) was the first to inoculate the bean with spores of another anthracnose fungus in order to determine whether the forms occurring on different hosts were really the same species. He sowed

on green bean pods the spores of *Gloeosporium castagna* Mont., which had proved to be very virulent on the leaves of the silver poplar, but obtained no infection. He therefore concluded that gloeosporial forms are independent species and have their own host plants. Southworth (1890:48) attempted unsuccessfully to infect bean pods with the hollyhock-anthracnose fungus, *Colletotrichum althaeae* Southw. (*C. malvarum* [A. Br. & Casp.] Southw.), but was successful with *C. lindemuthianum*. Halsted (1893 b:327, 329), in connection with his cross-inoculation work, obtained good infection on detached bean pods with *Colletotrichum* sp. from the eggplant, and with Gloeosporia from pepper, apple, and tomato; also (1893 d:248) with *Colletotrichum lagernarium* (Pass.) E. & Hals. from the watermelon. Sheldon (1904:132-135) inoculated wax-bean seedlings, bean plants in blossom, and bean pods on the plants, and also six different cucurbits, with spores of *C. lagernarium* from pure cultures obtained from a watermelon fruit. Infection was obtained on the cucurbits in most cases, but the beans for the most part were free from evidence of infection. Sheldon did find, however, spots bearing spores both on the beans inoculated by him and on those used as checks. He decides that it is not safe to conclude from his results that the anthracnose fungus on the beans is the same as that on the melons and the gourds. Edgerton (1910:41) obtained no infection on young bush beans sprayed with spores of the fig anthracnose (*Glomerella fructigena* [Clinton] Sacc.) and of the pepper anthracnose (*G. piperata* [E. & E.] S. & S.), and no infection on freshly picked bean pods placed in a moist chamber and inoculated with a culture of the rose-anthracnose fungus (*Gloeosporium rosae* Hals.); although in every case good infection was obtained with the bean-anthracnose fungus on the beans used as a control. Bean seeds wet with a suspension of spores of the fig- and the cotton-anthracnose fungus were somewhat infected. Spores of the fig-anthracnose fungus were being produced in abundance on seed that had rotted in the ground, and the semi-living cotyledons of the germinating beans were attacked by both fungi. The spots did not develop further, however, while in the case of seeds treated in the same way with spores of the bean-anthracnose fungus the cotyledons, and later the plants, became highly infected. Taubenhaus (1911:198) reports success in obtaining infection on pods of pole and bush lima beans in the field from puncture inoculation with spores of species of Gloeosporium from sweet pea, apple, and mandrake, or may-apple, and with

Gloeosporium officinale E. & E. from sassafras, *G. gallarum* Ch. Rich. from oak gall, and *G. psidii* Del. from guava. The disease produced, except in the last-named case, resembled sweet-pea anthracnose but did not resemble the bean disease. Shear and Wood (1913:77–89) inoculated detached bean pods with anthracnose conidia from avocado, cotton, guava, loquat, mandarin, orange, pitcairnia, and privet, but in the case of none of these did they obtain any infection. Krüger (1913) inoculated detached bean pods kept under bell jars with conidia of gloeosporial forms from apple, banana, and tomato, and, while good infection was obtained on checks consisting of detached fruits of the respective hosts, the result on bean pods was doubtful; no infection was obtained on the uninjured pods, although there was some mycelial growth in the tissue surrounding the injury made on other pods. Gardner (1918:23) inoculated five varieties of beans with *Colletotrichum lagenarium*, with negative results.

On inoculating bean seedlings of several varieties with spores of the anthracnose fungus from sweet pea and from mandrake, the writer did not obtain any infection. Fair infection was obtained on sweet-pea seedlings inoculated with spores of the form from sweet pea, and on the leaves and stems of young mandrake plants growing in the woods and of those transplanted to the greenhouse inoculated with the form from mandrake. From his own results and from those obtained by others, the writer is inclined to believe that, in general, each of the various anthracnose fungi is confined to its own host or to closely related plants.

ECOLOGIC ASPECTS

In the preceding discussion frequent reference has been made to weather conditions favorable to infection. There is no question that the weather is an important factor in the growth of this fungus, just as it is in the growth of higher plants. The fungus has its ups and downs according as the season is wet or dry. Temperature and humidity are the two factors of greatest importance, and of these the latter is usually the controlling one in the Northern States. This has been generally recognized by growers, and its significance in the development of the disease has been pointed out in some of the earlier accounts.

Edgerton (1910:28, and 1915:248) has shown that temperature is the controlling factor under conditions in Louisiana. The disease, while

prevalent during the cooler part of the growing season, is absent from the fields there during the hot months of June, July, and August, even with ample rainfall and when diseased seed was used for planting. Furthermore, Edgerton experienced great difficulty in keeping cultures of the organism alive during the summer. The writer has never had any difficulty in obtaining infections from inoculations made during the summer, although for the success of the experiments he has made them at times when the conditions promised to be most favorable. Some of the inoculations were made in the greenhouse when the temperature during the following days ran high, and yet fair to good infection was obtained in several instances. Cultures of the fungus in the laboratory grow very slowly or not at all during the excessively warm weather of the summer, and in some cases they die when not transferred frequently. When placed in a cellar where the temperature remained at about 16° to 20° C., a good growth of mycelium and abundant production of spores resulted. During the summer season in the North, the periods of excessively high temperatures are short. The high temperature of the day is not sufficient to kill the fungus in the host, and growth and spore production may take place during the lower temperatures of the night. The effect of temperature on growth of the fungus in culture media has already been discussed (page 121). Lauritzen (1919 20), by employing inoculation chambers where temperature and humidity were controlled, determined the range of temperatures at which infection of bean seedlings takes place after inoculation with *Colletotrichum lindemuthianum*, when kept at a favorable constant degree of humidity, to be from 57° to 80° F. At the extremes the number of infections occurring are small, but they are more abundant at the more nearly optimum temperatures, as one would expect. Lauritzen says that the data point to a lower temperature limit for infection when forty-eight hours are used for the infection period than when twenty-four hours are used.

Moisture must be present or the humidity of the air high if the fungus is to gain entrance to the host. Lauritzen (1919:29) found that infection took place at humidities of 95.8 and above when the temperature was kept at from 65° to 68° F. It was not necessary that a film of moisture be kept on the leaf during the germination of the spore, for infection occurred when the plants were dried off after inoculation and before being placed in the inoculation chamber. Lauritzen did not determine how

the spore gets sufficient water in such cases to permit germination, but he suggests that when the evaporation is not too great it may absorb water from the host plant by imbibition and later by osmosis.

If the soil is wet and cold, the bean seed germinates slowly, but the spores of the fungus when present on the seed under such conditions will germinate and penetrate the host before it appears above ground. If dry weather follows the appearance of the plants grown from spotted seed and infection has not yet taken place, the chances are good that the spotted cotyledons will drop off before any infection occurs. When this happens the plants are as free from infection as though they had come from healthy seed, but the affected cotyledons on the ground may serve as a source of inoculum for a time. Often after wet weather the juvenile leaves of the seedlings become very badly spotted. These in turn drop off, and if the plant has not been infected otherwise it may continue to develop entirely free of the disease (fig. 17). If, on the other hand, rainy weather should occur following the germination of spotted seed and before the cotyledons fall, some of the seedlings will surely become infected and the disease will be likely to spread to neighboring plants. In fact, an instance is known in which, of two fields planted from the same lot of seed but at different times, one field became badly diseased and the other remained healthy because rainy weather succeeded the planting of the one and dry weather the planting of the other.

If infection is to take place in plants inoculated with the spores of the fungus, a moist condition must prevail for at least eighteen consecutive hours at some time before the spores succumb to desiccation so that they may germinate and form appressoria. This statement is based on spore-germination tests recorded earlier (page 117). In the inoculation experiments conducted by the writer, the plants were usually kept in an inoculation chamber for about forty-eight hours, although successful results were obtained when they were left for but twenty-four hours. That the spores may endure a period of dryness before favorable conditions arrive was shown by an experiment in which seedlings growing outdoors were inoculated during the morning of a bright, hot day. The next morning, before the dew had evaporated, each plant was covered with a shaded lamp chimney plugged with cotton at the upper end. All these plants showed lesions after six days.

FIG. 17. BEAN PLANT FROM SPOTTED SEED, THE JUVENILE LEAVES AND STEM OF WHICH BECAME AFFECTED WITH ANTHRACNOSE BUT WHICH PRODUCED A CLEAN CROP OF PODS BECAUSE DRY WEATHER PREVAILED DURING THE SUMMER

(Transplanted to a pot for photographing)

A rainy period of several days accompanied by cool weather is the most favorable condition for infection and for the development of the fungus. Night dew or even humid air, however, is sufficient to allow infection to take place. Conditions permitting the plant to retain moisture beneath the vines are particularly favorable for the infection of the pods. Such conditions are afforded by poor soil drainage, or especially by poor air drainage such as may come about from a bushy growth of vines and from plants growing close together; and similar conditions may exist in a low area or pocket in the field.

Beans grown at the time of the year when the prevailing weather conditions are the least likely to be favorable for infection, will of course be the freest from anthracnose. Plants inoculated artificially during a rainy day will become badly diseased, while plants in neighboring hills in the same row will be but slightly affected and hills farther on not at all. This is because the weather has remained comparatively dry from the time of inoculation until the pods were maturing, and thus spore dissemination was prevented. The disease does not spread as readily through a field planted in check rows as through one planted in drills. Corbett (1907) says that growers of field beans find the disease worse on crops planted early. In New York State late-maturing beans are the most liable to damage from anthracnose, as weather conditions favorable for infection commonly occur during September. For this reason an early-maturing variety planted early would have a better chance of escaping infection, other things being equal, than a late-maturing one.

These facts explain why the disease materially decreased during the dry seasons of the four years from 1907 to 1910, and why it has been so severe during years of abundant rainfall. The seed produced in dry seasons is practically free from the disease, and when such seed is used the plants resulting therefrom are remarkably free from anthracnose, even though the season may be wet, because the source of infection is not present. After a season or so of rainy weather, however, the disease, at first inconspicuous, may become general throughout the field and a large amount of spotted seed may result. It has been claimed by seedsmen that in certain irrigated sections of the West where there is but little rainfall during the growing season, plants free from the disease can be grown from spotted seed; but it is questionable whether the moist conditions between the vines resulting from irrigation would not be sufficiently

favorable for infection occasionally to take place, at least when spotted seed is planted. The disease is occasionally reported from such sections. Complete freedom from anthracnose may be expected in those regions where dry farming is practiced. Lauritzen (1919:32) suggests that the variation in the amount of moisture in the air in different regions may be an important factor in the distribution of diseases over the earth's surface.

PROPHYLACTIC ASPECTS

As early as 1893 a number of measures for the control of bean anthracnose had been recommended. Among these were such as treating seed with chemicals or hot water, selecting seed from healthy plants, spraying with bordeaux mixture and other substances, working among the plants only when they are dry, planting exclusively on ground that has not produced diseased plants the year before, and selecting a dry, airy situation with light soil. These recommendations, if carefully followed, will usually result in the production of plants free from anthracnose. Doubt has been cast, however, on the efficacy of certain of these recommendations, and it is worth while to consider the advantages and disadvantages of the various methods.

Seed disinfection

Seed treatment was first recommended by Halsted (1892:286), who at that time used ammoniacal copper carbonate. Later (Halsted and Kelsey, 1895:30) he tried full-, half-, and quarter-strength bordeaux mixture, and concluded that such treatment had but little effect in killing the mycelium within the seed. Beach (1892:320), after experimenting with hot water, bordeaux, ammoniacal copper carbonate, and potassium sulfide, found that, while hot-water treatment resulted in the lowest percentage of plants with anthracnose, the untreated seed gave a greater quantity of marketable beans because of the better stand, and that even with severe treatment enough disease remained to injure the crop. Craig (1893), after soaking seed for varying lengths of time in solutions of different strengths of ammoniacal copper carbonate and copper sulfate, concluded that seed can be treated cheaply and advantageously with copper compounds, preferably ammoniacal copper carbonate. The best result he obtained, however, was but 79 per cent of healthy plants, and but 73 per cent of the treated seed germinated. Later (1898) he experimented with lysol,

formalin, potassium sulfide, nitrate of soda, corrosive sublimate, and kainit. The lysol treatment resulted in 4 per cent of diseased pods, in comparison with 57 per cent in the check row. The value of other treatments are in the order named, corrosive sublimate giving 19 per cent of diseased pods and kainit 36 per cent. Bedford (1900) soaked bean seed for two hours in formalin solutions varying from one ounce in one gallon of water to one ounce in four gallons. The former dilution gave the better results, without the germination being affected appreciably. Sevey (1907) states that experiments at Cornell University, in which bean seed was soaked for forty-five minutes in formalin solution 1-200, gave profitable results. Kirk (1905) says that good results have been obtained by soaking seed for five minutes in water at a temperature of 140° F. (60° C.), or for fifteen minutes in water at 130° F. (54.4° C.).

Wheizel (1906) believes seed treatment to be of little practical value in controlling the disease, as such treatment reduces the stand and renders the seeds unfit for planting with a machine unless they are allowed to dry, in which case many of them slip their coats and thus become worthless. Fulton (1908 15) says that he has kept beans for forty-five minutes at 135° F. (57.2° C.) dry heat without appreciable effect on germination, while seeds placed in water during a like exposure are practically all killed. He thought that dry heat might be used as a seed treatment for control of bacterial blight, but experiments that he made to prove this gave negative results. Edgerton (1910 46 48), from experiments he has made, is inclined to believe that the disease may be materially reduced by soaking the seed for from ten to fifteen minutes in water at a temperature of 50° C. (122° F.), and that seeds thus treated will not slip their coats and their germinative ability is not impaired. Later, Edgerton and Moreland (1913) report that the treatment of bean seed with hot water 50° C. for eight minutes, with corrosive sublimate solution 1-1000 for twenty minutes, with benetol solution 1-50 for twenty minutes, or with corrosive sublimate 1-1000 in a 1-50 glycerin solution, did not materially reduce the percentage of germination below that of untreated seed, although formaldehyde solution 1-100 did reduce the germination in the field. However, none of the treatments except hot water had much merit as a control measure for anthracnose, although blight was materially reduced by the treatments with corrosive sublimate and benetol.

Hollman (1915:691) treated seed with 2.5- and 1.25-per-cent Chlorphenolquecksilber, with 1- and 2-per-cent sublimate, with 2.5- and 4-per-cent formalin, with a tar preparation called "Körnerschutz," with petroleum for thirty minutes, and with 2-per-cent copper sulfate, and also with 1-per-cent bordeaux sprayed on the seeds. None of these treatments were effective, the disease being serious in all plots. The Chlorphenolquecksilber seemed to have the effect of stimulating the plants to increased growth, so that they yielded more, in spite of the disease, than did plants in other plots.

Fischer (1919:249) discusses the results obtained by a number of investigators with seed treatment. He says that Appel used 1-per-cent sublimate; Remn and Vasters tried Chlorphenolquecksilber; Wahl tried a new and water-free Chlorphenolquecksilber called "Uspulun"; Wurth experimented with sublimate and later with Uspulun; Schander and Krause treated badly affected seed, which when untreated gave only 19.3 per cent germination, with 1-per-cent sublimate for fifteen minutes, resulting in 29.3 per cent germination; with 0.25-per-cent Chinosol for three hours, resulting in 32 per cent germination; and with 5-per-cent Uspulun for one and one-half hours, resulting in 46 per cent germination. In no case, however, was there a satisfactory control of the disease, which became general throughout all the plots. Even when an entire field of the experiment station was planted with treated seed — in which case infection could not have taken place from near-by plants from untreated seed — the disease appeared just as severely as in fields planted with untreated seed. Fischer concludes from these observations that seed treatment of beans to control anthracnose has no practical value.

Muncie (1917:26-37) treated seed for varying lengths of time with chemicals of varying strengths, and with both dry heat and hot water. The chemicals used were: mercuric chloride and sodium nitrate heated to 55° C. (131° F.) and not heated; mercuric chloride alone; mercuric chloride with oxalic acid; zinc chloride; formaldehyde solution as a dip and sprinkled on seed; formaldehyde gas; copper sulfate with the addition of sulfuric acid; and calcium hypochlorite. Both healthy seed, and seed affected with anthracnose and with blight, were treated, and the effect of the treatment on germination and on the pathogenes was noted. It is seen from the results given that in none of the treatments was either pathogene killed in all the seeds, except in those cases in which the

treatment materially reduced the percentage of germination. Muncie states, in summing up the results of the treatments, that it seems possible to control the disease in a large degree in case of a light infection by employing seed treatments, and that the treatment most efficient is either a thirty-minutes immersion in a 35-per-cent solution of bleaching powder, or a sprinkling of the seed, as in the treatment of oat smut, with a solution of formaldehyde, using 1 pint of formaldehyde to 30 gallons of water. There is not sufficient evidence submitted in his data, however, to admit this possibility. His summary at the end of the bulletin states accurately the conclusions reached, namely, "Seed treatments with chemical solutions and wet and dry heat have failed to control these diseases." Rapp (1920) concludes from his numerous seed-treatment experiments with formaldehyde, mercuric chloride, sulfuric acid, dry heat, and hot water, to control bacterial blight, that no present method can be regarded as satisfactory, since in killing the blight pathogene the germinating power of the seed is either greatly weakened or totally destroyed.

Kidd and West (1918) soaked bean and other seeds for varying lengths of time (from six to seventy-two hours), and found that, while germination was more rapid from soaked than from unsoaked seeds, subsequent growth, particularly of the bean, was poorer — although with horse beans (*Vicia faba*) it was greatly improved. Bean seed was soaked in water at various temperatures, but always the resultant growth was poorer than when dry seed was used. The literature on the subject, however, reviewed by Kidd and West (1919), indicates a better growth and a higher total yield from soaking in a limited quantity of water.

Further experimentation with seed treatment should not be regarded as something bound to be resultless. No one has made a careful study of the permeability of the seed coat of the bean to various disinfecting agencies, nor of the action of these agencies on the fungus within the seed. Seed treatment, to be effective, must destroy the pathogene within the seed, notwithstanding the extent of its growth there, in order that the affected seed may not serve as a source of inoculum. At the same time the treatment must not injure sound seed. Any treatment, to be of value, must achieve these two conditions, and the problem does not appear to be insurmountable. Nevertheless, healthy seed can be obtained in other ways. The selection of clean seed (page 168) certainly offers a better promise of success.

Sorting out affected seed

The selection of clean seed has been recommended by many plant pathologists. Frank (1883b: 523), after having determined that infection of the seedling can take place from the fungus overwintered in affected seed, was the first person to recommend the use of clean seed by the sorting-out of spotted ones or by the securing of seed from non-infested fields. Beach (1892: 323-326) obtained good results by sorting out the affected seed before planting. Gain (1898: 200), after experimenting with Mont d'Or, a climbing wax-podded variety with dark brown seeds, states that he is able to discard practically every diseased seed by hand-sorting. He observes that diseased seeds are lighter than healthy ones, and advises growers to discard all light seed. In another article (1899: 389) he says that by carefully sorting out infected seed the anthracnose disease can be controlled. Whetzel (1908: 432), however, although he used the utmost care to remove every suspected bean, was unable to remove the diseased seed completely from white beans, a germination test of the seed thus sorted showing as many as 12 per cent of the remaining seed diseased. When an attempt is made to sort colored seed, an even larger percentage of diseased seed passes unobserved. Fischer (1919: 252) concludes from experiments conducted by Schander and Krause, and from other tests made at Bromberg in 1915 and 1916, that it is not possible to control the disease by this method since many affected seeds cannot be detected from their appearance.

It is, of course, impossible to sort out every affected seed even by the most careful examination. Such seed as are left in may produce affected plants if conditions following planting are favorable for the development of the fungus, and such affected plants may serve as a source of inoculum to other plants in the field. However, as every diseased seed discarded removes one source from the field, it would appear to be preferable to sort the seed carefully before planting rather than not to sort at all. A practical grower of a considerable acreage of beans in northern Vermont says that since he has made a practice of hand-sorting his seed he has had no anthracnose, but that before he did so the disease was harmful.

Selecting seed from clean pods

It has occurred to a number of experimenters that the surest way of obtaining clean seed is to select it from healthy plants or at least from

unspotted pods. Harvey (1894) advises this method, and emphasizes the idea that pods showing any evidence of disease, such as pits, discolored patches, and wrinkled or blistered places, should be rejected. Cobb (1894: 383) recommends hand-picking the seed in the field, selecting only the healthiest-looking pods. Several others since then have recommended the practice. For several years Whetzel (1908: 441) grew clean Black Wax beans that were selected from clean pods, and at a time when anthracnose was very prevalent throughout the State. He recommends selecting seed from clean pods, hand-picking them in the field, and resorting them later. He suggests also that seed from the irrigated regions of the West may possibly be free from the disease. A seedsman in an irrigated section of Colorado declares that he has been able to grow clean plants from diseased seed and could continue the practice without danger of the disease appearing in the field.

The writer selected seed from clean pods during four consecutive seasons (1908 to 1911), the purpose being to determine whether such seed would produce anthracnose-free plants with ordinary culture, particularly during a wet season, and whether such a method could be recommended as a general farm practice. Since 1911 he has been unable to carry out these trials further, except in a most limited way.

The seed for these experiments was obtained from pods picked in the field, or in a few cases from the mow. Any seeds showing evidence of anthracnose or blight were rejected. Later the pods were resorted, and, after shelling, the beans also were sorted to remove broken, undersized, or abnormal beans. The seed was then distributed, in lots of about a quart of each variety, to growers and experimenters in this and other States, in order to obtain, in some place at least, good conditions for a test. Those who received the seed were urged to plant it at a distance from other bean patches and to observe the precautions necessary to avoid communication of the disease to this seed patch.

In these tests extending over a period of four years, twenty-four different plots of beans, containing from one to eight varieties, were grown in various parts of New York State and in a few places outside the State. In five of these plots, there was some anthracnose on a few of the varieties. In all but one of these five cases the infection was slight, and in all cases the inoculum came from a source other than the seed.

The chief drawback to the success of the trials was the dry weather which prevailed during the growing season in these years. Beans grown from seed that had not been selected produced anthracnose-free plants in many cases. Plants grown by Dr. Edgerton in Louisiana from healthy seed sent to him were free from anthracnose and with few exceptions free from blight, while other beans grown in the trucking section were badly affected with both anthracnose and blight.

Another factor not given consideration at that time was the resistance of many of these varieties to at least one strain of the pathogene. It was learned later that this is true of the varieties Navy Pea, White Kidney, Red Kidney, Red Marrow, and Blue Pod Medium, and also of Turtle Soup to some extent. In most instances, however, anthracnose had in the past appeared in a destructive manner on the varieties sent for testing, in the localities under consideration.

The introduction of healthy seed of a certain variety into a locality in which the strain of the fungus to which it is susceptible is absent, would of necessity result in an anthracnose-free crop. This may be the reason why clean seed from other sections of the country often produces better yields than does home-grown seed. However, if affected seed of such a variety is introduced into a certain locality, the strain of the pathogene present on the seed, being capable of producing the disease in that variety, will multiply under conditions favorable for it and the entire crop may become diseased. Healthy seed is therefore always safer to use as long as the particular variety is susceptible to any strain of the organism.

In 1914 Professor F. C. Stewart, of Geneva, New York, planted seed that he himself had selected from clean pods. The plants remained healthy all summer and the pods were free from anthracnose when picked. A patch of Red Kidney and Turtle Soup beans selected from seed from clean pods in 1912 was planted at Ithaca at a distance of ten rods from other beans artificially inoculated with the two strains of *Colletotrichum lindemuthianum* during the summer. The plants from clean seed remained free from anthracnose.

In 1915 Bert Smalley, of Interlaken, New York, grew one row, fifteen rods long, of Red Marrow beans from seed selected from clean pods by Professor Stewart and afterward resorted by him in order to be sure there was no anthracnose present. The field in which this row of Red Marrows was grown was not cultivated at all during the season because of wet

weather, and so weeds of various kinds grew up among the bean plants On October 4 the plants were found to be generally affected with anthracnose. From the row 75 plants were selected, one plant at every pace. On these plants there were 209 pods, of which 137 were affected with anthracnose, 67 were not spotted, and 5 were doubtful. About 40 rods southwest of the end of this row was a large field of Red Kidney beans which were badly affected with anthracnose. It was concluded that the first infection of plants in the row planted with clean seed came from spores carried from the affected Red Kidneys by some animal, and, since the tall weeds about the beans kept them moist most of the time during the rainy season, and since they were planted in drills so that the plants were in contact with one another, the disease readily spread along the entire row.

These trials seem to indicate that the use of clean seed is not altogether successful in producing a crop of beans free from anthracnose unless the season is dry, under which condition there is no loss from the disease in any field. The experiments are reported because the results are such as may be expected in such cases. So far as observations were made in these and in other experiments, clean seed always produced anthracnose-free seedlings in the field, and this is all that can be expected of clean seed. Infection, when present, must have taken place from an inoculum of a source other than the seed. In some cases this came early from old affected vines or from near-by affected plants. Infection will always be likely to occur from such sources under favorable weather conditions unless precautions are taken to prevent it. Since clean seed can be depended upon to produce seedlings free from anthracnose, the question becomes one of deciding whether or not the presence of affected seedlings in the field is a sufficiently great menace to warrant the use of clean seed. The writer, from observations of his own experimental plots and of many fields in which clean seed as compared with affected seed has been used, is convinced that the presence of such affected seedlings is a menace that warrants the grower's going to considerable pains and expense in order to obtain healthy seed. Growers generally will probably prefer to buy clean seed if they can get it, rather than to take the trouble to produce it. But some one must produce it if it is to be had, and the question of production is the one concerned here. It is true that following dry seasons there will be but little difficulty in obtaining

bean seed almost or quite free from anthracnose. But it must be possible to obtain such seed every year if the disease is to be avoided in years favorable for its appearance. The practice of selecting from clean pods is the only reliable way to secure seed free from anthracnose (figs. 18 and 19). The method in its practical application involves the use of a seed plot, on which the selected clean seed is planted. This plot should

FIG. 18. A HILL OF WAX BEANS FROM SPOTTED SEED

The pods are so badly affected with anthracnose that they are worthless

produce the necessary seed for planting the main field the following year. The steps in carrying out the measure are as follows:

1. Selection, in the fall, of pods having no anthracnose or blight spots. These should be shelled by hand or with a flail, and the seed afterward sorted over to remove all discolored, impure, undersized, shriveled, or broken beans. The amount of seed to be selected in this way will depend on the amount needed for planting the main field. If 40 bushels of seed are required for planting the main field and 20 bushels an acre can be

expected from the seed plot, then enough seed must be selected from clean pods to plant two acres.

When the main field contains 200 acres or more, the size of a plot necessary to produce sufficient seed for the main field will be so large that

FIG. 19. A HILL OF WAX BEANS FROM HEALTHY SEED
The pods are entirely free from anthracnose

it will be difficult to obtain by pod selection enough seed to plant it. In such a case it is desirable to maintain an increase plot in addition to a small seed plot. The seed plot would be used to provide clean seed for the increase plot, which in turn would produce sufficient seed for the

main field. This plan would require two years to get seed for the main field, but would afterward permit an economy of time and effort.

2. Location of the seed plot at a considerable distance, preferably 40 rods or more, from other bean fields or garden patches containing beans. If an increase plot is used, it should be located at some distance from the seed plot and also at some distance from the main field. This is to prevent, as far as possible, the transfer of spores of the causal fungus from infected plants to plants in the seed plot. The shorter the distance between the seed plot and beans growing elsewhere, other things being equal, the greater is the chance that the beans in the seed plot will become inoculated.

3. Location of the seed plot and the bean field on soil on which beans were not produced the preceding year.

4. Cultivation of the seed plot before the cultivation of other beans when the same tool is used for both; or, better, reservation for the seed plot of a cultivator not used in other bean fields.

5. The precaution of not visiting the seed plot when vines or soil are wet. This precaution should apply to all bean fields. Care should be taken, even when the vines are dry, not to go directly into the seed plot from other bean fields.

6. Prompt removal and destruction of any plants in the seed plot found to be affected with anthracnose.

7. Application of bordeaux mixture to the plants in the seed plot several times during the season, in order to prevent infection from spores that may be carried there.

8. Selection, before the beans are harvested, of clean and otherwise desirable pods from the seed plot or other fields, in order to obtain healthy seed for planting the succeeding year's seed plot.

9. Careful harvesting of the bean plants in the seed plot and their storage in a place separate from other bean vines.

10. The threshing of the beans with a flail or in other ways so that a mixture with other bean seed cannot take place.

11. Storage of the seed in a cool, dry place until planting time the succeeding year.

12. Careful hand-picking of this seed for the increase plot or the main field in order to remove all discolored or otherwise unsatisfactory seed.

This method of controlling anthracnose in the main field will cost less than spraying five times, and is more certain of success. Much of the procedure costs nothing, but merely requires not doing certain things. The labor involved in growing a 40-acre field of beans by this method, above that ordinarily required for growing such a field, consists in selecting sufficient seed for a seed plot, in spraying the vines in this plot, in removing affected plants from it when present, in the separate harvesting and threshing of the crop, and in the careful hand-picking of the seed from it. Other work done in connection with the seed plot would have been required had it been a part of the main field.

If home-grown seed is as good as or superior to that purchased elsewhere, then growers of a large acreage of beans who have felt the loss from anthracnose, or seed dealers who are desirous of obtaining the best possible seed for their territory, should give consideration to this method. It is not to be expected that many farmers will adopt such a method, because of the detail required in order to insure success. It should be pointed out here that this method cannot be depended upon absolutely to control bacterial blight. Burkholder (1921:67) states that as a result of systemic infection of the bean plant the seeds may become infected without the pods around them showing any evidence of blight.

Procuring seed from localities where anthracnose does not occur

Observations were made for two seasons (1908 and 1909) of fields planted with Colorado-grown and eastern-grown Refugee Wax bean seed. There was no anthracnose but considerable blight present in the field planted with the western seed, while anthracnose was present to some extent in the field planted with the eastern seed. The seed procured from Colorado the second year was dry and split easily, and besides it germinated poorly, and so the yield was lower than that from the eastern seed. Edgerton (1910:50) has planted Colorado seed in Louisiana and has found it freer from anthracnose than most other seed, though much more severely affected with bacterial blight. Muncie (1917:41) reports trials in Michigan of seed grown for one year in the States of Washington, Idaho, and California. There was a little anthracnose in the seed returned from Washington but none in that from the other States. Idaho-grown seed gave very satisfactory results the first year but poor results the second year, largely because the seed was immature due to an early frost.

California-grown Early Wonder seed gave excellent results, and the plants ripened two weeks earlier in Michigan than did plants of the same variety from seed grown in Idaho and from seed grown in Michigan. Muncie believes that carefully selected seed sent to southern California to be grown for one year for seed purposes, will furnish a supply of seed year after year that will be superior to Michigan-grown seed.

Edgerton (1910 28–37) states that at the high summer temperatures in Louisiana, bean anthracnose does not develop even when spotted seed is planted; and later he suggests (Edgerton and Moreland, 1913 17) that Louisiana truckers grow their own bean seed during the summer as a second crop and thus secure seed freer from disease than that purchased from the North.

The question whether eastern growers would have better success in buying western seed than by the use of eastern-grown seed is still unanswered. It must be considered from other standpoints as well as from that of controlling anthracnose. It is true that this disease does not occur as commonly or cause as much damage in the West as in the East. It was, however, rather prevalent in Colorado in 1916 and 1917, and to an extent sufficient to cause some spotting of the seed. Bacterial blight occurs rather commonly in the West, so that one cannot depend on western seed being free from this disease. Nevertheless, eastern seedsmen have found that they can depend upon getting good seed from the West oftener than from the East, and the bean seed-growing industry has developed rapidly in Colorado and Idaho in recent years. Most of the seed beans grown are garden and canning varieties, which command a much higher price in the East than the ordinary field sorts.

Avoiding conditions favorable for the dissemination and growth of the fungus

If it becomes necessary to plant seed having a small percentage of anthracnose infection, or if the disease appears in the field from an outside source of inoculum, or even when clean seed is planted, it is advisable to avoid as far as is practicable those conditions which favor the spread of the pathogene. Healthy plants have been grown from clean seed in experimental plots in the same field with plants that have become badly diseased from artificial inoculation with the anthracnose fungus. It has been observed also in a large number of instances that plants in hills next to inoculated plants often did not become infected although

the weather was favorable for infection to take place. The disease did not spread because certain conditions favorable for it were not allowed to exist. Some of the precautions to be taken are considered in the following pages.

Manner of planting

Beans planted so close together that they form a dense mat of vines favor the spread of the disease. The vines obstruct cultivation and do not allow either the wind or the sunshine to dry out the moisture beneath them. Spores of the pathogene, if present, are transferred from one plant to others in contact, and are able under the moist conditions to germinate and penetrate the tissues of the host without difficulty.

The different varieties vary so much in their habit of growth and in the size of their seed that it is impossible to give a general recommendation for planting. Halsted (Halsted and Kelsey, 1895:28, and Halsted, 1897: 290) planted seed from 3 to 24 inches apart in rows 20 inches apart. There was a considerable decline in the proportion of spotted pods and also in the total yield of pods as the distance between the plants was increased. Halsey concludes that 4½ inches is the most satisfactory distance for Golden Wax beans. Ferris (1909:8) recommends, in addition to selecting clean seed, planting the beans in bunches in the row far enough apart so that the clusters do not touch one another. Edgerton (1909:5) finds three beans to the hill, and the hills 18 inches apart, a very satisfactory planting distance for beans grown in Louisiana. Fischer (1919) says that Riehm suggests planting in hills 50 by 50 centimeters apart instead of in drills, in order to permit good air drainage. Von Diakonoff (1909) suggests planting the rows parallel to the direction of the prevailing winds in order that the plants may be well aerated.

Anthracnose will not spread through a field of beans planted in hills as rapidly as it will through one planted in drills, because the vines in one hill are somewhat isolated from vines in other hills for a considerable part of the season, whereas in drills there is a continuous row of plants in contact with one another, and anthracnose starting at any point in the row would, under favorable conditions, spread the entire length. To secure maximum protection by hill planting, the hills should be far enough apart each way so that the vines of one hill will not come in contact with vines of other hills; and this distance will vary with different

varieties. Of course the yield in such a case will be reduced below that obtained when a greater amount of seed is used, but not proportionately. It is impracticable, however, to plant hills at a distance sufficient to keep the vines of one hill from touching those of others during the latter part of the season. Just what distance apart the hills of any variety should be planted in order to secure a satisfactory yield and protection from infection has not been determined. Whatever has been said on this subject should be considered also in the light of present knowledge concerning the possibility of spore dissemination by spattering.

Good land drainage

The relation of drainage to bean anthracnose is obvious. Poorly drained soil is cold, and bean seed planted in such soil starts slowly or not at all. If the seed is diseased, the fungus develops rapidly and usually destroys the seedling before it appears above ground. During a wet season poorly drained soil tends to produce a moist condition about the base of the plants, which should be avoided. Galloway (1889) notes that the disease is worse on moist soil. Cobb (1894:383) and Querner (1908), in recommending control measures for the disease, suggest draining the land, and others suggest not choosing low, damp ground.

Removal of affected seedlings

Affected seedlings serve as a source of infection to healthy plants in the field and the garden. An early removal of them would aid in lessening the amount of disease should favorable weather for infection follow. The practice of removing affected plants was early recommended. Berkeley (1880) suggests that diseased plants be pulled and burned, and many other writers on the subject have recommended this. Wheeler (1908:433), however, has pointed out that this method is absolutely impracticable except in short garden rows. It is, of course, out of the question to attempt to remove affected seedlings from a field. However, in the seed plot and in the garden it is worth while to remove and destroy such plants, as is explained later. If the weather remains dry following the appearance of the seedling, the diseased cotyledons will drop off before further infection of the seedling takes place, as already noted (page 161). In such a case the field would be as free from disease as though every diseased seedling had been removed. Appel (1916 has

observed that hilling young plants tends to prevent the spread of the disease by covering the lesions at the base of the stem, thus hindering the spores from escaping. The small lesions heal afterward, and, while the larger ones may develop and rot the plant, the spores produced are not able to be disseminated. Edgerton (1909:5) suggests that danger of the disease's spreading from affected seedlings may be lessened if the field is not entered until the cotyledons have dropped off.

Leaving the plants untouched while wet

As has been noted (page 176), a diseased plant may exist in a field of beans without the disease spreading materially to other plants. If, however, when the plants are wet, some agent passing through the field comes in contact with the diseased vine, spores are likely to be distributed to plants beyond. A very active agent in distributing spores is a horse and cultivator, or, even more so, a person picking beans. Growers of a large acreage like to start work in the fields early, and yet there are many mornings during the growing season when the dew remains on the plants until after nine o'clock. It is very important that operations in the bean field should be postponed until the vines are dry. The observance of this simple precaution will do much toward preventing a general infection of the field

Destroying diseased vines in the fall

Since the fungus lives over winter on the old pods and vines, these may serve as a source of infection to young beans growing near them the following spring. Galloway (1889) recommends the burning of all diseased vines and pods. Both Harvey (1894) and Cobb (1894:383) believe it advisable to remove and destroy all diseased vines after harvest if the same land is to be used for beans the following year. Whetzel (1906:209) states that diseased pods and stalks should be removed from the field. The old vines and pods are not so often a source of inoculum as are the affected seeds, and yet it is unwise to disregard them altogether. One should not go to a considerable expense to remove and destroy old affected vines from the field, but should prevent their coming into contact with the new crop as far as it is practicable to do so. A rotation of the bean crop, and the application of manure containing bean refuse to other than the current or the following year's bean field, are helpful measures.

Planting at a time of the year when anthracnose is least likely to be present

Corbett (1907) suggests late planting as a possible means of avoiding the disease. This may do very well where the growing season is long, but in New York State the varieties usually planted require practically all the growing season to properly mature their pods. Since the months of July and August are drier on the average than the other months of the growing season, early-maturing varieties planted at the beginning of July might be less likely to be affected with anthracnose than if planted earlier, as the disease would not have as good an opportunity to develop from affected seeds. There are so many other factors of importance in deciding the time of planting, however, that this one of preventing anthracnose can be given little consideration.

Planting early-maturing varieties

There are years when anthracnose does not become prevalent until the fall rains come on, so that an early-maturing variety would escape infection. A variety of white pea bean known as Early Wonder is recommended by Muncie (1916) to Michigan growers because it ripens from ten to fourteen days earlier than other varieties of this kind, and thus matures before diseases have made serious invasion into the tissue of the pod, with consequent spotting of seed. This bean does not ripen appreciably earlier in New York than does the ordinary Navy Pea.

Spraying

It is interesting to note that even before the discovery of bordeaux mixture, the application of a fungicide to bean pods for the control of anthracnose had been made. Frank (1883b, 523) found that flowers of sulfur greatly decreases the number of cases of infection but provides no real security against the disease. Scribner (1888, 364) states that under some circumstances applications of solutions of sulfate of iron or of copper may be made, but their use on the fruit cannot be generally recommended because of their poisonous character. He suggests the use of liver of sulfur, one ounce to five gallons of water. Galloway (1889) recommends a very early application of hyposulfite of soda, one ounce to one gallon of water, or of potassium sulfide, one-fourth ounce to one gallon of water. Two subsequent sprayings should be made after the pods are from one-half to two-thirds developed.

Five years after the introduction of bordeaux mixture into the United States, several investigators recommended its use for the control of bean anthracnose. Beach (1892:314–317, 326) experimented with cupric borate, cupric polysulfide, and bordeaux mixture. The last-named was much superior to the others and increased the yield to nearly double that of unsprayed plants. Beach emphasized the importance of spraying thoroughly and of using a nozzle that would produce a misty spray. He believed that the addition to the mixture of enough soap to make suds would cause the mixture to form a thin film over the leaves instead of minute drops. McCarthy (1892:14) recommends either an iron sulfate or a potassium sulfide solution with lime, to which molasses or glue is added as a sticker. He recommends also, as a substitute for the spray solutions, a dust mixture composed either of sulfur flour or precipitated copper carbonate diluted with some dry powdered material, as air-slaked lime or wheat flour. He believes that the application should be made as soon as the flowers have withered if there is any disease in the neighborhood. Halsted (1895 [Halsted and Kelsey] to 1901) carried on spraying experiments with beans for seven years. He used a large number of fungicides, including lime-bordeaux of various strengths, soda-bordeaux, potash-bordeaux, ammoniacal copper carbonate, eau céleste, creolin, and potassium sulfide. Soap also was used in combination with copper sulfate and with eau céleste. Halsted found that there was little difference between the regular bordeaux and the soda-bordeaux in their effects, but the other fungicides proved inferior and creolin was practically worthless. When anthracnose and blight were prevalent they were reduced materially, in most cases, by spraying with bordeaux. With the two successive crops of 1896 (Halsted, 1897:330) and the two of 1897 (Halsted, 1898:310, 312), the check row yielded more beans than did the sprayed rows. During the dry seasons of the year 1900 (Halsted, 1901 b:420, 421), little or no success was obtained from spraying. Whetzel (1906 208) relates an instance in which a single spraying reduced the amount of anthracnose 90 per cent. Blin (1906) obtained relatively good results in France during 1901 and 1902 from spraying with bordeaux. Von Diakonoff (1909) advises bordeaux or a copper-sugar-lime mixture.

County agricultural agents have occasionally reported instances in which spraying has given good results in preventing the disease. Nearly all the spray calendars and bulletins on the subject issued by the various

experiment stations include spraying with bordeaux mixture in their recommendations for control of bean anthracnose. In later years, instances have occurred in which bordeaux was reported as not successful in controlling the disease although the vines were well sprayed.

Fairchild (1894), White (1906 95), Corbett (1907), and Whetzel (1908 433) question the practicability of spraying beans generally, although granting that there may be circumstances under which it could be recommended. Whetzel has succeeded, however, in controlling the disease on a few rows by thoroughly and properly applying the mixture with a hand machine. He says that the field machines are not constructed so that the mixture can be applied as thoroughly and effectively as by hand. He believes that until a machine is put on the market capable of delivering a spray that will cover the stems and the pods at any stage in the growth of the plant, little or no results can be expected from spraying, and even then the practice will be very expensive because of the machinery, chemicals, and labor involved. Hollman (1915) sprayed plants grown from affected seed with 1-per-cent bordeaux mixture without much success, but he advises its use as a protective measure. Fischer (1919, 249) tells of Schander and Krause's experiments at Bromberg, where a 1- or 2-per-cent soda-bordeaux and a 1- or 2-per-cent lime-bordeaux were used. The soda-bordeaux killed the plants and the lime-bordeaux injured them, at least when the solution contained just enough lime to neutralize the copper sulfate solution. Later experiments with 1-per-cent bordeaux, even when seed from healthy pods sorted from diseased plants was used, reduced only slightly the number of affected pods and did not prevent the disease from appearing on the leaves and stems.

The writer conducted spraying experiments during the years 1908 and 1909 in large fields of canning beans at Oneida, New York, in cooperation with the Burt Olney Canning Company, in small experimental plots at Oneida during 1908, 1909, and 1910, and at Ithaca, New York, for six years after 1910. The field sprayings were conducted on 200 acres or more of beans. These were sprayed five times during the growing season, at intervals of about ten days, the applications beginning when the plants were just out of the ground and continuing until after picking had begun. Bordeaux mixture (4-4-50) was used on part of each field and lime-sulfur (1-50) on another part, the two sprayed areas being separated by fifteen unsprayed rows. With the varieties of beans grown, Refugee Wax and

Refugee Green Pod, the pods and the undersides of the leaves, which are the particular points of attack, are so protected by their bushy growth that it is very difficult to apply the mixture thoroughly to these places with the ordinary field sprayer. A Niagara gas sprayer was used and the mixture was delivered at 100 pounds pressure from near the ground to the sides of the plant (fig. 20). Two and sometimes three machines were kept busy during the spraying season. In 1908 the company expended $1000 for bean spraying alone, and in 1909 the expenditure was $1250. Each application cost about $1 an acre. Thus the spraying

FIG. 20.—PLATFORM AND APPARATUS FOR PREPARING BORDEAUX MIXTURE IN LARGE QUANTITIES, AND SPRAYING MACHINE DEVISED ESPECIALLY FOR SPRAYING BEANS

question was of sufficient importance to the officials of the company for them to wish to have its value demonstrated, and this in spite of the fact that they had been spraying for the past seven years.

A calculation of the yield, and of the amount of anthracnose and blight, on the three center unsprayed check rows and for the three bordeaux-sprayed rows adjoining, was made at each picking of every field. A calculation of the yield of plants sprayed with lime-sulfur was made from only a few fields.

The amount of anthracnose and of blight during the two years was negligible. The difference in yield between sprayed and unsprayed rows was slight, being one year in favor of the sprayed rows and the following

year in favor of the unsprayed, and in both cases being well within the range of experimental error. The company has since discontinued spraying beans.

During the eight years since 1908 a few rows of beans have been thoroughly sprayed with bordeaux, and a few with lime-sulfur, a hand machine being used. From four to six thorough applications were made throughout the season, beginning soon after the plants appeared and continuing until the pods were about two-thirds grown. The first year neither anthracnose nor blight appeared to any appreciable extent, even on the check rows. In 1909 no anthracnose was present, but the blight appeared to be controlled somewhat by the application of the spray. With one variety, Refugee Green Pod, there was no blight on the sprayed rows while in the unsprayed rows 3 per cent of the pods were spotted with blight. On the Red Marrows that were sprayed 2 per cent of the pods were spotted with blight, while the unsprayed rows had 11 per cent of spotted pods.

In 1910 both anthracnose and blight were again negligible. In 1911 one-third of each of six rows was planted on June 22 to seed of several varieties mixed together, all badly spotted with anthracnose. Mixed varieties were used because it was not possible to obtain a sufficient quantity of affected seed of one variety. The remaining two-thirds of the six rows were planted at the same time to seed selected from clean pods, three rows to Red Marrow and three to Navy Pea. The first and fourth rows were sprayed with bordeaux, the second and fifth rows were not sprayed, and the third and sixth rows were sprayed with lime-sulfur. Powdered arsenate of lead at the rate of 2 pounds to 50 gallons was added to both the bordeaux and the lime-sulfur, in the hope of killing insects that might be instrumental in carrying the blight organism. Five applications were made during the season, on June 13, July 1, 14, and 25, and August 9. One-half of the plants in that part of the plot farthest from the end planted to spotted seed were inoculated with a suspension of spores of two strains of *Colletotrichum lindemuthianum* which had proved virulent on the two varieties. This left one-half of the plants from clean seed as a middle third of each row uninoculated with the fungus in any way except with spores that might be carried to them. Two inoculations were made, one on July 17 when one-half of the plants set aside for this purpose were inoculated, and the other on August 22, when the remainder

ere inoculated. These inoculations were made at times when the weather romised exceptionally favorable conditions for infection, and it proved to be in each case. The plan of the experiment may be outlined as follows:

Application	Clean seed		Spotted seed, plants not inoculated artificially
	Plants inoculated artificially	Plants not inoculated artificially	
rdeaux I	Red Marrow	Red Marrow	Mixed varieties
t sprayed I	Red Marrow	Red Marrow	Mixed varieties
ne-sulfur I	Red Marrow	Red Marrow	Mixed varieties
rdeaux II	Navy Pea	Navy Pea	Mixed varieties
t sprayed II	Navy Pea	Navy Pea	Mixed varieties
ne-sulfur II	Navy Pea	Navy Pea	Mixed varieties

The spotted seed was largely of the wax type, and the pods were picked hen a majority were of marketable size as string beans. The results on this experiment are given in table 7. The healthy pods, after being rted out, were left in a basket for three days. They were then sorted ain and the percentage of pods that had spotted in the meantime was

BLE 7. YIELD, AND PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND BLIGHT, ROM SPRAYED AND FROM UNSPRAYED ROWS OF SNAP BEANS GROWN FROM SEED BADLY SPOTTED WITH ANTHRACNOSE, IN 1911

Treatment	Date of picking	Number of plants in row	Number of healthy pods	Pods spotted with anthracnose (per cent)	Pods spotted with blight (per cent)	Additional pods spotted with anthracnose after being picked three days (per cent)
deaux I	August 13	62	307	0 6	1 2	0 3
k I	August 13	71	663	1 7	6 7	20 0
esulfur I	August 13	62	380	1 8	12 8	0 0
deaux II	August 17	71	722	4 0	0 1	3 3
k II	August 17	70	557	18 8	4 5	10 7
esulfur II	August 17	82	502	2 0	1 5	0 5

determined. No importance is attributed to the comparative yield number of pods given in table 7, as the seed was mixed and more plan of a prolific nature may have been present in one row than in another.

It is seen from table 7 that there was a decided control of the disea by spraying with either bordeaux or lime-sulfur. The control is especiall noticeable on pods three days after picking.

The results with field beans grown from healthy seed are given in tabl 8. It is seen from this table that spraying the vines with either bordeau or lime-sulfur materially reduced the percentage of spotted pods due anthracnose. The spraying does not appear to have controlled the blight

The pods sprayed with bordeaux in the above experiments were decided discolored by the precipitate from the mixture. Fawcett (1907) point out that this may be avoided by making the last application with ammonia cal copper carbonate, which leaves no stain. The pods sprayed wi lime-sulfur showed no evidence of stain at picking time.

In 1912 complete results from spraying were obtained from only small plot, two-thirds of which consisted of Red Marrows planted wi seed from clean pods while the other third of each row was planted wi spotted seed of mixed varieties. The planting was done on June 1 and applications of fungicides were made on July 7, 17, and 26, and Augu 6. Bordeaux (4–4–50) and lime-sulfur (32° Baumé, 1 50) were th fungicides used. The results are given in table 9. From this table it i seen that no control of anthracnose was obtained from spraying, as that seeds from clean pods were nearly as badly affected as those fro spotted seed. Earlier in the season (July 26), however, the plants fro clean seed had shown practically no infection, but infection was common on the plants from spotted seed. Cool, rainy weather during Augus brought about abundant infection from numerous sources.

In 1913 spraying was done on seven varieties planted in eleven plot 50 feet long. Plots 1, 2, and 3 were planted with seed a small pe centage of which was spotted with anthracnose; plots 4, 5, 6, 7, 8, and 9 wit seed a large percentage of which was similarly spotted; and plots 10 an 11 with seed from selected clean pods. The planting was done on June 29 The Red Valentine and Challenge Black Wax beans did not germinate well and were replanted on July 12. Applications of fungicides were made on July 16 and 26, and August 6 and 16. The Navy Pea and Red Kidney

TABLE 5.—YIELD AND PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND BLIGHT, FROM SPRAYED AND FROM UNSPRAYED ROWS OF FIELD BEANS GROWN FROM SELECTED HEALTHY SEED, IN 1911

	Variety	Treatment	Number of plants	Yield of dry pods (grams)	Yield of seed (grams)	Pods spotted with anthracnose (per cent)	Pods spotted with blight (per cent)	Clean pods (per cent)	Spotted seed (per cent)
Not inoculated artificially	Red Marrow	Bordeaux	52	1,255	806	25.0	6 5	68 5	0 0
		Check	58	1,335	947	76 0	0 0	24 0	18 0
		Lime-sulfur	56	1,045	765	20 0	3 5	76 5	10 0
	Navy Pea	Bordeaux	49	936	704	0 0	5 0	95.0	0 0
		Check	47	935	715	36 0	11 0	53.0	10 0
		Lime-sulfur	48	1,115	850	12 0	14 0	74.0	1 0
Inoculated artificially twice during season	Red Marrow	Bordeaux	114	2,525	1,830	33 0	5 3	61 4	0 0
		Check	118	2,055	1,455	82 0	1 0	17.0	21 0
		Lime-sulfur	118	2,010	1,452	27 5	5 5	67.0	17 0
	Navy Pea	Bordeaux	92	1,575	1,220	4 0	5 5	90 5	1 0
		Check	90	1,610	1,215	49 0	4 5	46.5	10 0
		Lime-sulfur	92	1,675	1,275	24 0	5.0	71 0	3 5

beans, since they would mature later, were given another application on September 8. Bordeaux (5-5-50), Pyrox (1 pound to 5 gallons of water, as recommended on the label), and lime-sulfur (32° Baumé, 1–50), were

TABLE 9. YIELD, AND NUMBER AND PERCENTAGE OF RED MARROW BEAN PODS SPOTTED WITH ANTHRACNOSE, FROM SPRAYED AND FROM UNSPRAYED ROWS IN 1912

Seed planted	Treatment	Number of pods	Pods affected with anthracnose	
			Number	Per cent
Clean seed	Bordeaux	2,600	2,450	93
	Check	1,452	1,450	99
	Lime-sulfur	1,983	1,950	98
Spotted seed	Bordeaux	392	392	100
	Check	227	227	100
	Lime-sulfur	295	295	100

the fungicides used. A killing frost occurred on September 15. Only the percentage of pods spotted with anthracnose is given in table 10, showing the results:

TABLE 10. PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE IN SPRAYED AND IN UNSPRAYED ROWS, FROM ELEVEN PLOTS CONTAINING SEVEN VARIETIES OF BEANS IN 1913

Plot	Variety	Treatment			
		Bordeaux	Pyrox	Not sprayed	Lime-sulfur
1	Red Kidney	0 0	0 0	0 0	0 0
2	Crystal Wax	*2 4	*0 2	*1 4	*1 0
3	Red Valentine	0 0	0 6	0 0	0 0
4	Challenge Black Wax	0 2	0 8	57 2	0 8
5	Navy Pea	0 4	0 4	0 4	0 4
6	Red Kidney	4 6	6 2	58 6	17 4
7	Crystal Wax	0 2	7 0	36 4	20 8
8	Golden Wax	0 0	0 0	0 0	0 0
9	Refugee Wax	0 0	0 0	0 0	0 0
10	Red Kidney	0 0	0 0	0 0	0 0
11	Navy Pea	0 0	0 0	0 0	0 0

* The cotyledons showed anthracnose lesions.

The season was dry and anthracnose was not abundant, but the results n plots 1, 6, and 7, the only ones having a considerable amount of anthrac- ose in the checks, lead to the conclusion that the fungicides were effective the following order: bordeaux, Pyrox, lime-sulfur, with the latter falling ort somewhat.

Spraying was continued during 1914 on Refugee Wax, Davis Wax, Flageolet Wax, an unidentified wax, and Burpee's Stringless Green Pod. ows 50 feet long of each variety were planted on June 2, on plots situated de by side on the same land that was used for this purpose in 1913 able 11). The Flageolet Wax contained a large percentage of seed spotted ith anthracnose, but the seed of the other varieties included only a nall amount of spotted seed. The row of Flageolet Wax had many issing hills. Applications of the fungicides were made on July 2, 15, d 26, and August 9. One row of each variety was sprayed with bordeaux -5 50), one row of each, except the unidentified wax, with Pyrox (1 pound 5 gallons of water), and one row of each except Flageolet Wax and e unidentified wax with Sulfocide, a commercial sulfur solution (1 gallon 200 gallons of water). The remaining row of each variety was left nsprayed as a check.

In order to insure anthracnose infection, two inoculations with spores *Colletotrichum lindemuthianum* obtained from cultures were made, e on August 2 and the other on August 16. Favorable weather for fection followed in each case, and the weather at Ithaca during the mmer continued favorable for the development of the pathogene. ll the varieties matured their pods before frost and a record of healthy d spotted pods was made on October 8 (tables 11 and 12).

This experiment shows that all the spray materials used had value in e control of anthracnose and blight. The plants from spotted seed were adly affected, and the control of the disease by spraying was not so od on them as on plants from clean seed.

n 1915 but one variety, Davis Wax, was used in the spraying experi- nt. Two rows 50 feet long were planted on June 8, one to be sprayed l one to be left as a check. One-third of each row was planted h seed of this variety spotted with anthracnose, and the other two- rds with seed from selected clean pods. A thorough natural inoculation ok place, and so it was not necessary to inoculate artificially. The beans

appeared on June 16 and applications of a fungicide were made on June 19, July 3, 10, 24, and 30, and August 7. Pyrox (1 pound to 5 gallons of water) was used for the first three applications and bordeaux 5-5-50

TABLE 11. YIELD, AND NUMBER AND PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND WITH BLIGHT, IN SPRAYED AND IN UNSPRAYED ROWS IN 1914

Variety	Treatment	Total number of pods	Pods spotted with anthracnose		Pods spotted with blight	
			Number	Per cent	Number	Per cent
Refugee Wax	Bordeaux	1,120	3	0.3	5	0.5
	Pyrox	1,134	10	0.9	3	0.3
	Check	1,467	129	8.8	7	0.5
	Sulfocide	1,307	93	7.1	4	.31
Davis Wax	Bordeaux	612	33	5.4	12	2.0
	Pyrox	475	19	4.0	11	2.3
	Check	344	23	6.6	59	17.2
	Sulfocide	173	10	5.8	27	15.6
Flageolet Wax	Bordeaux	74	6	8.0	5	6.8
	Pyrox	90	23	25.8	3	3.3
	Check	174	151	86.8	1	.23
Unidentified wax	Bordeaux	506	20	4.0	5	1.0
	Check	252	46	18.3	13	5.2
Burpee's Stringless Green Pod	Bordeaux	776	76	9.8	10	1.3
	Pyrox	670	40	6.0	9	1.3
	Check	641	131	20.3	28	4.3
	Sulfocide	411	55	13.4	27	6.6

TABLE 12. AVERAGE PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND WITH BLIGHT FROM THE VARIOUS SPRAYED AND UNSPRAYED PLOTS ON THE RESPECTIVE VARIETIES EMPLOYED, IN 1914

Treatment	Anthracnose (per cent)	Blight (per cent)
Bordeaux	5.5	2.3
Pyrox	9.2	1.8
Check	28.2	5.9
Sulfocide	8.8	5.1

of the other three, the change to bordeaux being made because of the injury resulting to the vines from the use of Pyrox; three hills, in fact, were killed, and the others on July 15 looked very straggling from the loss of their lower leaves, so that they presented a much less satisfactory appearance than the unsprayed rows, even though they were but little affected with anthracnose. The results of this experiment are given in Table 13.

TABLE 13. YIELD OF DAVIS WAX BEANS, NUMBER AND PERCENTAGE OF PODS AFFECTED WITH ANTHRACNOSE, AND WEIGHT OF GOOD AND OF CULL SEEDS, FROM SPRAYED AND FROM UNSPRAYED ROWS IN 1915

Seed planted		Sprayed	Not sprayed
Spotted seed	Number of plants	26	30
	Number of pods	122	129
	Number of pods affected with anthracnose	43	129
	Per cent of pods affected	35	100
	Weight of good seed (grams)	79	10
	Weight of cull seed (grams)	17	52
Clean seed	Number of plants	66	86
	Number of pods	240	521
	Number of pods affected with anthracnose	22	521
	Per cent of pods affected	9	100
	Weight of good seed (grams)	290	89
	Weight of cull seed (grams)	49	410
Total	Number of plants	92	116
	Number of pods	362	650
	Number of pods affected with anthracnose	65	650
	Per cent of pods affected	18	100
	Weight of good seed (grams)	369	99
	Weight of cull seed (grams)	66	462

This experiment, although not conducted on an extended scale, shows conclusively the control that can be obtained by spraying the plants heavily with bordeaux mixture a sufficient number of times during the season to protect them.

Spraying was continued in 1916 on Davis Wax and Refugee Wax beans. Two rows 40 feet long of each variety were planted on June 10; spotted seed was used in one-third of each row, and healthy seed in the remainder. No artificial inoculations were made. One row of each variety was left

unsprayed as a check, and one of each was sprayed with bordeaux mixtur (5–5–50) on July 3, 12, and 24, and August 3, 14, and 24. Data obtaine at harvest, October 4, are given in table 14:

TABLE 14. YIELD OF DAVIS WAX AND REFUGEE WAX BEANS, AND NUMBER AN PERCENTAGE OF PODS AFFECTED WITH ANTHRACNOSE, FROM SPRAYED AND FROM U SPRAYED ROWS IN 1916

Variety	Treatment	Number of plants	Total number of pods	Pods affected with anthracnose		Weight of good seed (grams)	Weight of all seed (grams)
				Number	Per cent		
Davis Wax	Sprayed	59	520	93	18	652	6
	Not sprayed	61	437	184	42	175	5
Refugee Wax	Sprayed	80	770	16	2	870	10
	Not sprayed	71	662	121	18		

It seems to the writer, in view of the results of these experiments, th anthracnose and possibly blight may be kept in check by thoroughly spra ing the plants with bordeaux mixture, if the operation is begun soon after the plants have appeared above ground and continued at intervals of about ten days until the pods are reaching marketable size. The nature of the growth of the plants determines to a considerable degree whether they may be sprayed well with a spraying machine. Varieties such as those used in the field experiments at Oneida are so bushy that it is very difficult to spray them thoroughly, while such varieties as Crystal Wax Currie, Davis, Detroit, Double-Barrel, and others, which have a more erect growth, although compact, are less difficult of such treatment.

The field experiments at Oneida show conclusively that it does not pay to spray during a dry season. Spraying experiments conducted on a small scale with hand sprayers have shown that it is possible to control the disease to a considerable extent by this method. Whether the disease can be controlled as well with traction or power machines during epiphytotic years is yet an unsettled question.

In regions where anthracnose usually occurs annually, spraying can probably be used to advantage if the practice is supplemented by the use of clean seed. In New York spraying is not practicable for growers of dry beans, and probably not for growers of canning beans. If the total cost of making five applications is $7.50 an acre, it would be necessary for growers of dry beans to get from spraying an increase of 1.5 bushels an acre each year with beans selling at $5 a bushel in order to balance accounts. A decided increase in yield could be expected in a year when anthracnose was prevalent, but none if the season were dry. If an epiphytotic of the disease occurs in two out of seven years, as was the case from 1908 to 1915, then it would be necessary for the grower to get an increase from spraying of about 5.25 bushels in each of such two years in order to come out even. In order to make spraying pay, he must get a greater increase in yield or the selling price must be greater, and the time spent in spraying must not be at the expense of other farm operations.

Applying a fungicide to picked pods before shipping

Rolfs (1897) recommends the application of a sulfur spray just before packing pods for shipping, in order to kill the spores adhering to the pods. Fawcett (1907) also recommends the application of either potassium sulfide or a soda-sulfur spray. He says the pods should be spread out on the floor and the spraying solution thoroughly applied, the pods being turned over during the operation so that all the surfaces will be covered. The pods should be allowed to dry before being crated. In order to guard further against infection, Kirk (1905) suggests the exclusion of affected pods in packing, and Fulton (1908, 12) says that affected pods should not be picked, washed, nor packed with sound ones. Containers should be so devised as to allow good ventilation, and the pods should be stored in as dry and cool places as is possible. Since there will be no anthracnose infection on pods during shipment if the disease is controlled in the field, stress should be placed on such control.

Application of a fungicide to the soil

Halsted (1900a, 380) is the only investigator who has ever recorded the application of any fungicide to the soil in an effort to control bean anthracnose, and in his experiment there was no anthracnose on any of his bean

plants throughout the season although blight was present to some extent. He applied bordeaux mixture to the soil at the rate of 4320 gallons to the acre. In the first crop of the year the blight was reduced one-half on leaves and pods, but in the second crop there was just as much blight on these plants as there was on the check. Moreover, the plants growing on land that had received the application were smaller than those on the untreated soil.

Rotation of crops

The idea that the fungus is able to winter in the soil has led many writers to recommend, among other suggestions, that the grower should not plant beans on land that bore a diseased crop the previous season. Harvey (1894, 153) calls attention to this, and in the same year Cobb (1894) advises a change of ground. Halsted (1900 b: 127), after growing beans each year on the same ground for a number of successive years, found that the plants yielded more in the first four years than when grown on new land, but less afterward. Usually a greater number of spotted pods were produced on plants grown year after year on the same land.

Observations were made by the writer on beans grown as the seventh successive crop on the same land. They appeared as thrifty, and yielded as well, as any crop grown on rotated land. Moreover, they were as free from anthracnose and blight as the others, although in fairness it must be said that the summers had been dry for the three years preceding the observations. There is little chance of anthracnose occurring where beans are planted year after year on the same ground, if the vines, when affected, are not returned to this soil. There is greater danger that such a practice will introduce other diseases, especially stem rots, which tend to reduce the yield materially.

Selection of resistant plants

As has been stated earlier in this paper (page 149), no variety of *Phaseolus vulgaris* has been found to be absolutely immune to anthracnose, although a selection of the ordinary Red Kidney has been obtained which has proved to be resistant to such an extent that it will produce a very satisfactory yield in years when the ordinary Red Kidney becomes badly affected, and a Nova Scotia White Marrow has been located that shows considerable resistance in the field although susceptible in the seedling stage when inoculated artificially. Further progress in obtaining resistant

beans with these as a basis for hybridization is being made, the resistance being readily tested by artificial inoculation in the field, the cold frame, or the green-house. Selections can be made of large numbers of individuals by artificially inoculating them while in the seedling stage. Any showing marked resistance can be allowed to mature seed, and further tests can be made with them. Investigators are beginning to realize that the selection of plants resistant to disease is a most practical and satisfactory method of disease control, and even now work of this kind is engaging the attention of phytopathologists to a very marked degree.

As already stated (page 149), there are many varieties of beans which, while susceptible to one strain of the pathogene, are resistant to the other. It has been observed that often only one variety of beans is grown in a given locality; for example, Shepard (1919) reports that in 1918 pea beans constituted 76 per cent of all beans grown in Orleans County and 77 per cent of all grown in Monroe County, while in Yates County only 6 per cent of all beans are pea beans while 30 per cent are White Marrow, 29 per cent are Yellow Eye, and 15 per cent are Red Kidney. It happens that the pea bean referred to is susceptible to strain *alpha* of the pathogene but resistant to strain *beta*, while the other varieties mentioned are susceptible to strain *beta* but resistant to strain *alpha*. It is very likely that in regions where the pea bean is grown, strain *beta* does not exist to any great extent, and the introduction of clean seed of varieties resistant to this strain, even if susceptible to the other, would give crops of these varieties free from anthracnose for a few years. Eventually the *beta* strain would appear, and, its host being prevalent, would develop abundantly in years favorable for it. Similar results could be expected from the introduction of the pea bean, or any other variety resistant to the *beta* strain, into localities where this strain is the only one prevalent. There are other factors, to be sure, which tend to discourage a change in varieties in a given locality, and these have largely operated to prevent such changes.

Consideration of prophylactic measures

Bean anthracnose occurs to a serious extent in New York only during two or more wet seasons in succession, and the losses occasioned at such times are often forgotten by the grower in the dry seasons that intervene. It is a question with him then whether the time and the money needed for

successful control measures would not be lost in carrying them out. At the time when the disease occurs, however, he is willing to do anything to lessen its destructiveness. With bean anthracnose, as with most other plant diseases, control measures to be successful must be given consideration before the disease appears, or, better, before the crop is planted; and whatever measures are decided upon must be carried out completely. Frantic attempts to control the disease after it has appeared are usually a waste of time and money and cannot be generally recommended.

When one considers the various measures suggested for the control of this disease, he must realize that each has disadvantages and that the cost would be greater than the gain were all carried out even though the disease was thereby controlled. Some measures offer a greater promise of success than others. These are here summarized and briefly discussed.

Seed disinfection may prove to be worth while, but more experimental work is necessary before it can be recommended.

The avoidance of conditions favorable to the fungus is a precautionary measure that should receive consideration from all bean growers since it involves little or no expense.

Spraying is not a practicable measure for growers of dry beans in New York, but frequent and thorough applications of bordeaux mixture can be depended on to protect the plants from anthracnose; and such a control measure is practicable when the value of the crop is sufficiently great to warrant the expense involved.

As far as present evidence indicates, the application of a fungicide to the soil is impracticable and ineffective.

Rotation of crops, in itself, will not prevent anthracnose nor reduce the liability of its occurrence to any marked extent; but it is a measure that should receive some consideration, since its practice may serve to keep down the losses occasioned by other diseases.

The disinfection of picked pods need be considered only by growers of snap beans who ship to distant markets. This will not be necessary for growers who are successful in controlling the disease in their fields.

The use of anthracnose-resistant varieties is a satisfactory means of control and should be taken advantage of when possible.

The practice of careful hand-picking in order to remove diseased seed cannot be depended upon as an effective control measure because affected seed will escape the eye of the most practiced observer. However, this

practice will reduce the amount of affected seed planted, and if the seed is picked over at least twice the chances of getting a clean crop will be greatly improved as compared with the use of seed that has not been carefully hand-picked.

SUMMARY

Bean anthracnose is a disease of beans, principally affecting varieties of *Phaseolus vulgaris* L., which was first definitely reported and described in 1878 although it probably existed at a much earlier date. It has since been reported from every continent, and from nearly every country where beans are grown.

The disease has caused very large losses in years favorable for its development. In the eastern part of the United States, epiphytotics have occurred in the years 1906 to 1908 and 1914 to 1917.

All parts of the plant, even the roots, are subject to the disease, but it is most noticeable on the pods, where it forms dark, sunken cankers which subsequently extend to the seed contained within.

The spores germinate readily at room temperatures, within twenty-four hours in nutrient culture media and in bean agar and more slowly in water, the germ tube usually forming an appressorium on contact with a hard substratum.

A moderate growth of mycelium is produced in culture, which becomes dark-colored and forms acervuli from which a flesh-colored mass of spores is exuded. Under favorable conditions spores may be produced after three days growth. Cultures lose their power to produce spores by age or continued exposure to temperatures above the optimum. As the culture dries, setae are produced within and around the acervuli.

The minimum temperature for growth lies between 0° and 4° C., the optimum near 22°, and the maximum between 34° and a few degrees lower.

The fungus after entering the host extends its hyphae horizontally and diagonally into the cells. Browning of the cell contents occurs soon after the attack. The walls collapse and a lesion may be observed, at the earliest, four and one-half days after inoculation.

A stroma is formed at about the time when the cells collapse, and from it arise, in various places, a cluster of conidiophores which push up the epidermis, forming pimples. Spores are produced at the extremity of

the conidiophores, and these spores break through to the surface as a pasty mass. The fungus is capable of living from one season to another, and even for two seasons, in old affected vines and pods, which may serve as a source of inoculum when carried to the field. Spores washed into the soil are not viable to any extent after seven weeks.

The fungus when it invades the seed is able to live in its tissues in a more or less inactive condition for at least two years when the conditions of seed storage are not unfavorable for it.

Plants in the seedling stage and the youngest parts of older plants are the most susceptible to the disease.

There are at least two strains or biologic forms of the fungus. Many varieties of *Phaseolus vulgaris* resistant to the one are susceptible to the other, and vice versa. There are some varieties that are very susceptible to both strains, and at least one that is highly resistant to both. The wax-podded bush beans include a larger percentage susceptible to both strains than are found in other groups of varieties.

Several other species of Phaseolus are susceptible to anthracnose, but in this country, with rare exceptions, the disease is not severe or often noticeable on such plants.

A few species of the related genera Vigna (cowpea) and Dolichos (lablab and velvet beans) have shown some susceptibility in a few cases, but plants of other genera which have been inoculated have shown complete immunity.

Varieties of *Phaseolus vulgaris* are not susceptible to infection by fungi causing anthracnose of other plants, so far as infection experiments of them have been tried.

Selection of seed from clean pods has given a crop free from anthracnose in nearly all cases, and has always given anthracnose-free seedlings in clean soil.

Western-grown bean seed gave crops free from anthracnose but with considerable blight.

Spraying with bordeaux mixture throughout the season has prevented anthracnose to a large extent even in seasons favorable for it. In dry seasons spraying does not increase the yield. Applications of lime-sulfur solution and of two prepared fungicides gave some control, but not as good control as did bordeaux mixture.

The use of resistant varieties gave greatest promise of a satisfactory means of control.

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[1] *Cornell University Agricultural Experiment Station, Part II, Botany and Phytopathology*, the fourth preceding number of publications, was mailed on July 18, 1921.

[2] *Cornell University Agricultural Experiment Station, Plant Culture in Maine*, the third preceding number in this series, was mailed on July 19, 1921.

PLATE I

PATHOLOGICAL ANATOMY OF BEAN ANTHRACNOSE

1. Section across an [illegible] pod showing depth of lesion, affected tissue, and spore [illegible]. Drawn with aid of camera lucida. × 25

2. Section across [illegible] Refugee bean, showing an acervulus with spores and [illegible] setae. Drawn with aid of camera lucida. × 166

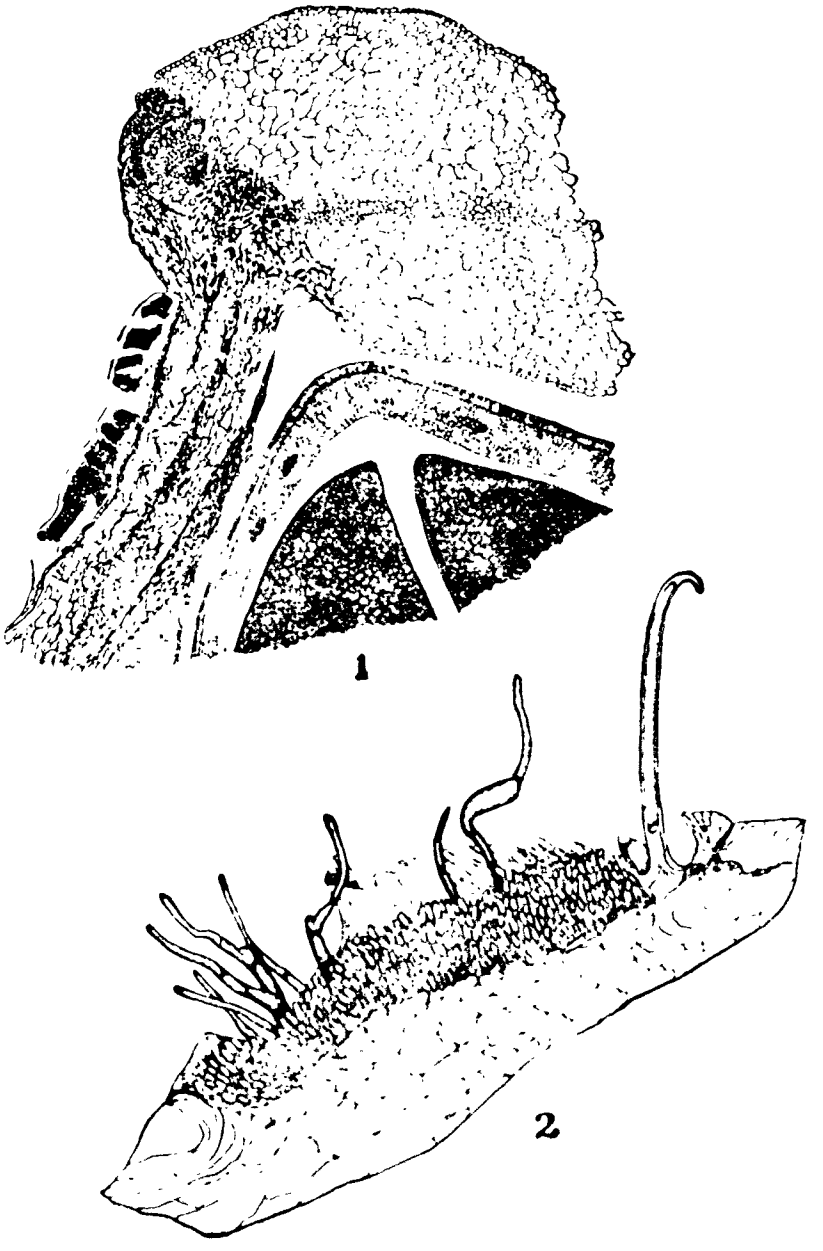
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PLATE II

DEVELOPMENT OF COLLETOTRICHUM LINDEMUTHIANUM WITHIN HOST TISSUE

1. Section of a pustule on Refugee Wax bean pod. The dotted area represents the fungus mycelium. Note the absence of fungus extending beyond the limits of the pustule and the ruptured epidermis. × 55.
2. Section of a pustule showing the formation of an epidermal cell over the fungus.
3. A few cells from the margin of a pustule on Refugee Wax bean pod showing the fungus.
4. Section of a portion of the outer coat of affected pod, showing twelve fungus hyphae penetrating the wall of a cell. × 550.

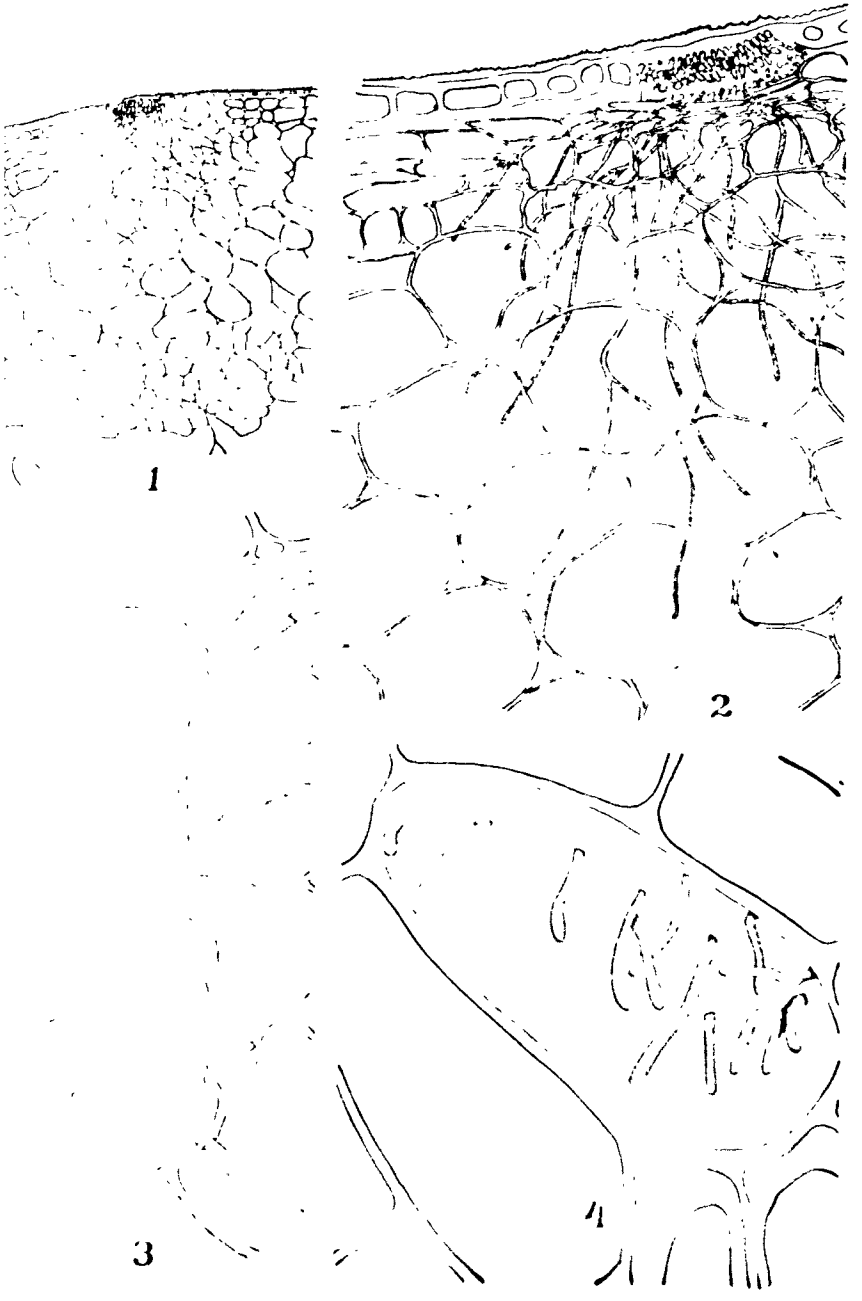
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PLATE III

CONIDIA OF COLLETOTRICHUM LINDEMUTHIANUM

Temperature was from 20 to 24° C.

1, Conidia from [illegible] showing [illegible] in bean agar, × 370. 3, Germ[illegible] after 30 [illegible] 4, Germination after 34 hours in agar, [illegible] 6, Germination after [illegible] hours in agar, [illegible] 7, [illegible] after 48 hours in agar, [illegible] × 847. 9, [illegible] after 24 hours in agar, [illegible] × 847. 10, [illegible] × 847. 11, After 57 [illegible] 12, After [illegible] hours [illegible] × 847. 13, After 9 days [illegible] 14, After 20 hours in distilled water, 15, After [illegible] hours in water, [illegible] 16, After 24 hours in rain water, × 360. 15. 17, After 38 hours in rain water, × 360. 15. 18, After 10 hours in rain water, × 847.

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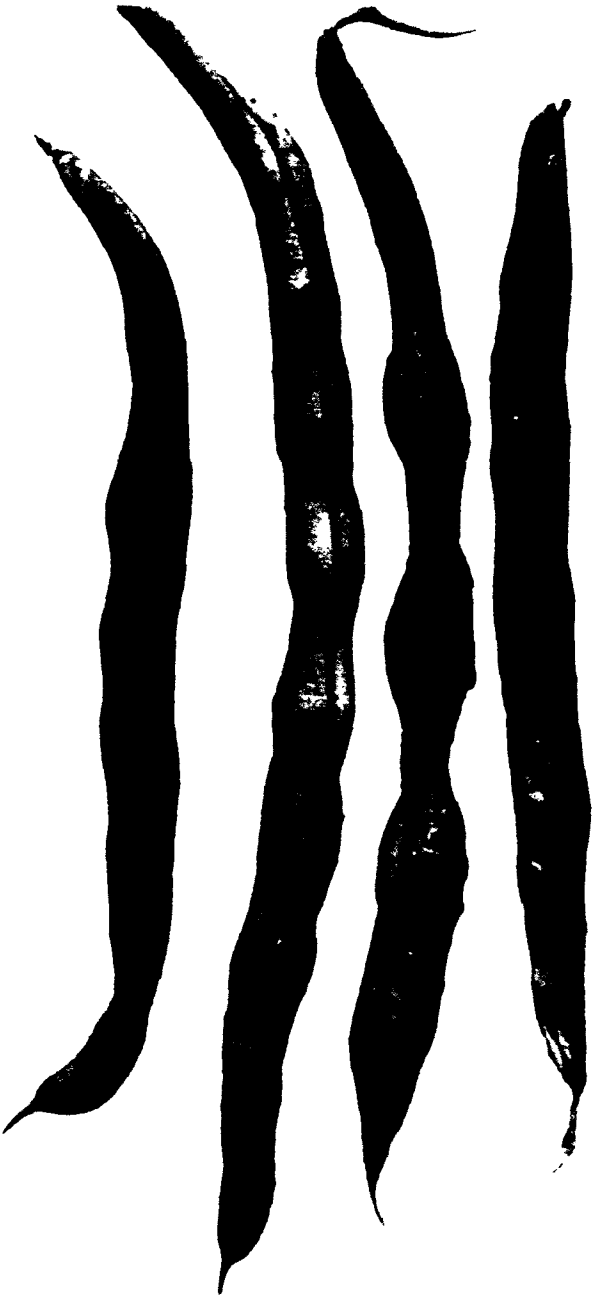
ANTHRACNOSE ON BEAN SEEDS

ANTHRACNOSE ON POD OF WAX AND GREEN-POD BEANS

BACTERIAL BLIGHT ON RED KIDNEY BEAN POD

RHIZOCTONIOSIS OF RED CLOVER, WAX BEAN POD



Rust (Uromyces appendiculatus) on bean leaves

.Y, 19?1 MEMOIR 43

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

RIATIONS IN BACTERIA COUNTS FROM MILK AS AFFECTED BY MEDIA AND INCUBATION TEMPERATURE

G. C. SUPPLEE, W. A. WHITING, AND P. A. DOWNS

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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BY MEDIA AND INCUBATION TEMPERATURE

VARIATIONS IN BACTERIA COUNTS FROM MILK AS AFFECTED BY MEDIA AND INCUBATION TEMPERATURE

G. C. Supplee[1], W. A. Whiting, and P. A. Downs

The increasing importance of the liquid-milk supply for large centers of population and the greater demand for a better quality of raw material for manufacturing purposes have necessitated further knowledge of the methods used in determining the quality of milk, and particularly have emphasized the significance of bacteriological analyses.

Examination of milk for the purpose of determining numbers or types of bacteria seems to constitute the highest ideal in milk grading. This aspect is doubtless important and the respect for this method of procedure in judging milk quality should not be endangered. Obviously, the sanitary aspects of the milk problem must involve determinations of this kind. The significance of bacteria in the economic phases of the milk supply also becomes quite clear when it is remembered that the entire business of supplying milk to the urban population is founded on modern dairy science, of which the aims are maximum wholesomeness and maximum keeping quality. These two considerations have been responsible for the stress laid on the importance of bacteria counts in the milk industry at the present time.

That the methods of enumerating bacteria in milk have many shortcomings is well recognized by dairy bacteriologists. Bacteria counts, as now obtained, can be interpreted only on a comparative basis, and in no sense do they indicate the mathematical accuracy which their expression in numbers implies. Such comparative interpretations can be used only as indications of degrees of success in handling and of the variations of keeping quality. Undeniably this information is valuable in safeguarding the interests of consumers of milk in large cities, and its importance is shown by the report of the Committee on Statistics of Milk and Cream Regulations of the Official Dairy Instructors' Association (1917).[2] This committee obtained the complete milk regulations from 409 cities and

[1] Director of Research Department of the Dry Milk Company, New York.

[2] See bibliography, page 247

towns in the United States, and found that 189 of these provided for legal limit for bacteria in milk sold within the municipality. The lim allowed by these cities ranged from 50,000 to 5,000,000 to the cubic cen meter, with approximately one-half of the cities permitting a limit 500,000. The necessity of fixing legal limits for bacteria in cream see to have been regarded as much less important, since only 30 of the cities had established legal limits for this product. The bacteria allow in the latter case varied from 50,000 to 1,000,000 to the cubic centimet

These municipal regulations must of necessity imply provisions for th enforcement and for penalties for failures in their observance. Su provisions immediately bring into prominence the difficulty of applicat and enforcement of numerical bacterial standards. Unfortunately, t inherent inaccuracies of present methods of enumerating bacteria are s great to permit their results to be relied upon with the certainty of exa ness which their fixed numerical standards would seem to warrant.

REVIEW OF PREVIOUS INVESTIGATIONS

The American Public Health Association (1915), recognizing the w variations obtained by the ordinary, plating technique, have formulat through their Laboratory Section, the following uniform method for det mining bacteria in milk. This procedure, known as the "Standa Methods of Bacterial Analyses of Milk," has been of considerable v in securing uniform technique in different laboratories, and the res are comparable, since a uniform interpretation can be given to them. T the purpose of the Standard Methods is for securing uniform res rather than accurate counts, in the minimum length of time, is evid from the fact that 37° C. for forty-eight hours on plain agar is the on incubation temperature and medium recognized. In the routine exa nation of milk samples, the short incubation period has certain distin advantages.

Conn (1915) compiled the results obtained from an exhaustive stu of comparative determinations made from the same milk by four labo atories. This work, involving many thousand platings made under t form procedure, nevertheless failed to give uniform and consistent resu under those particular conditions. Viewed from the standpoint of abs lutely accurate determinations of all bacteria present, there are numer

reasons why the plate method gives widely discrepant results. Among the most important causes are: (1) the failure of certain species to produce visible colonies on the medium and in the incubation temperature used; (2) the tendency of many species to exist in groups of two or more individuals, which groups are broken apart with varying degrees of completeness during the plating operation; (3) too few or too many colonies to the plate; (4) the inhibiting or beneficial effect of diffused by-products from the growth of certain species on other species within the radius of diffusion; (5) the personal element involved in carrying out the method. Widely varying results from the same sample of milk under the same conditions of incubation temperature and medium would still be caused by the clumping tendency, by the number of colonies on each plate, and by the personal element entering into the manipulations.

Hill and Ellms (1897) early called attention to the unreliable results obtained from over-crowded plates used in water analysis. The Standard Methods stipulate that there shall be not less than 30, and not more than 200, colonies to the plate, altho Breed and Dotterrer (1916) conclude the limits of 30 and 400 are nearly as satisfactory.

Altho the Standard Methods call for plain agar incubated at 37° C. for forty-eight hours, comparative counts published from time to time have shown that a carbohydrate medium and a longer incubation period at a lower temperature have many advantages. Hennemann and Glenn (1908), from their work on the effect of incubation temperatures and media, reached the following conclusions:

1. Since pathogenic bacteria are always difficult, and in most cases impossible, to find in milk, a high temperature of incubation has no advantage over room temperature from this viewpoint.

2. Incubation at 20° C. is superior to incubation at 37° C. because both a higher count and a better differential count are obtained.

3. Dextrose is preferable to lactose as an addition to the medium.

4. Milk is usually consumed before the results of bacterial examinations are available. Accordingly bacteriological and chemical examinations should have as their principal objects the improvement and control of the general supply; and accuracy being of greater importance than quick results, the loss of a day in its interest is irrelevant.

Sherman (1916) points out the higher counts obtainable by the use of lactose agar in place of plain agar, and also the increase in the size of the colonies and the better differentiation of the types.

Breed and Stocking (1917) published a preliminary report on a series of comparative determinations, in which they conclude that the plate method, when used by careful workers, will give more reliable results than those reported by Conn, which had been obtained under routine conditions and possibly, in some instances, by inexperienced operators. Obviously, inexperience and carelessness are factors to be avoided in any method of enumerating bacteria, especially when the results are for the determination of municipal regulations. The same authors (1920), reporting a similar but more extensive investigation, found the plate method and the microscopic method (Breed method) productive of reasonably uniform and accurate results for the total number of bacteria present, all factors known to introduce inaccuracies having been first reduced to a minimum. For the plate method they report an average coefficient of variability of 8.3, for the microscopic determination of groups of bacteria, consisting of one or more individuals, 11.7, and for the microscopic determination of individual bacteria, 13.4. Altho these results are remarkably uniform, it must be remembered that they are obtained from samples which were artificially inoculated in order to reduce the clumping tendency to a minimum and that the time and labor necessary to obtain this degree of accuracy by the microscopic method could not be expected in regular, routine examinations.

PRESENT EXPERIMENTS

Comparison of media and incubation temperatures

The experimental work reported herein was for the purpose of demonstrating the variations in counts obtained by plain and carbohydrate media at different incubation temperatures. It may indicate a partial reason why the count at 37° C. for forty-eight hours, as used in routine work, may be more subject to discrepancies than counts obtained from longer incubation periods at lower temperatures.

The samples used for this work were selected at random from the ordinary market milk of the Ithaca city supply, at intervals extending over a period of one and one-half years. Twenty-seven plates were made from the same dilution of each sample. Nine of the plates were

poured with standard plain agar; nine with nutrient agar containing 1 per cent of dextrose; and nine with nutrient agar containing 1 per cent of lactose. The different agars were all made from single, large-quantity batches of plain, nutrient agar. These were subdivided, and the definite percentage of the particular carbohydrate desired was added to each. Three of the nine plates containing the different agars were incubated at 37° C. for forty-eight hours; three at 30° C. for five days; and three at 20° C. for five days. With the exceptions noted, the technique given in the Standard Methods was carefully followed. It was necessary, however, to include counts from plates containing fewer than 30 colonies and more than 200 colonies, altho in all cases the dilution was designed to give colonies between these limits from the forty-eight hour count at 37°.

In table 1 are shown the counts obtained from 100 different samples of milk from each of the nine combinations of incubation temperatures and media. The individual counts appearing in this table are the averages of triplicate plates. Each plate of the series of three checked with the other plates of the series as closely as would be expected from duplicate or triplicate plates from the same dilution of any sample of normal milk. In order to indicate in a comprehensive manner the variations obtained, the 37° count was taken as the standard. Any variation above or below this count is indicated by a plus or a minus sign. The variations are shown also as percentages, the 37° count being accepted as 100 per cent, and counts higher or lower being indicated by figures above or below 100.

Sherman (1916) points out the higher counts obtainable by the use of lactose agar in place of plain agar, and also the increase in the size of the colonies and the better differentiation of the types.

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PRESENT EXPERIMENTS

Comparison of media and incubation temperatures

The experimental work reported herein was for the purpose of demonstrating the variations in counts obtained by plain and carbohydrate media at different incubation temperatures. It may indicate a further reason why the count at 37° C. for forty-eight hours, as used in routine work, may be more subject to discrepancies than counts obtained from longer incubation periods at lower temperatures.

The samples used for this work were selected at random from the ordinary market milk of the Ithaca city supply, at intervals extending over a period of one and one-half years. Twenty-seven plates were made from the same dilution of each sample. Nine of the plates were

poured with standard plain agar; nine with nutrient agar containing 1 per cent of dextrose; and nine with nutrient agar containing 1 per cent of lactose. The different agars were all made from single, large-quantity batches of plain, nutrient agar. These were subdivided, and the definite percentage of the particular carbohydrate desired was added to each. Three of the nine plates containing the different agars were incubated at 37° C. for forty-eight hours; three at 30° C. for five days; and three at 20° C. for five days. With the exceptions noted, the technique given in the Standard Methods was carefully followed. It was necessary, however, to include counts from plates containing fewer than 30 colonies and more than 200 colonies, altho in all cases the dilution was designed to give colonies between these limits from the forty-eight hour count at 37°.

In Table I are shown the counts obtained from 100 different samples of milk from each of the nine combinations of incubation temperatures and media. The individual counts appearing in this table are the averages of triplicate plates. Each plate of the series of three checked with the other plates of the series as closely as would be expected from duplicate or triplicate plates from the same dilution of any sample of normal milk. In order to indicate in a comprehensive manner the variations obtained, the 37° count was taken as the standard. Any variation above or below this count is indicated by a plus or a minus sign. The variations are shown also as percentages, the 37° count being accepted as 100 per cent, and counts higher or lower being indicated by figures above or below 100.

TABLE I. VARIATIONS IN COUNTS OBTAINED BY PLAIN AND CARBOHYDRATE AGAR AT DIFFERENT INCUBATION TEMPERATURES

Sample	Temperature C°	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
1	37	6,800,000		100	11,610,000	4,810,000 +	170	11,940,000	5,140,000 +	173
	30	7,080,000	280,000 +	104	11,790,000	4,990,000 +	173	10,580,000	3,780,000 +	156
	20	5,970,000	830,000	88	7,550,000	750,000 +	111	10,090,000	3,290,000 +	148
2	37	41,000		100	26,400	14,600	65	36,600	4,400	89
	30	41,500	500 +	101	38,400	2,600	93	38,600	2,400 -	94
	20	41,500	500 +	101	34,600	6,400	85	38,300	2,700 -	93
3	37	17,100		100	16,000	1,100	93	16,100	1,000 -	94
	30	21,200	4,100 +	124	17,000	100	99	18,800	1,700 +	110
	20	23,100	6,000 +	135	18,700	1,600 +	109	16,700	400 -	98
4	37	10,300		100	7,100	3,200	69	9,300	1,000 -	90
	30	14,900	4,600 +	145	14,000	3,700 +	136	13,100	2,800 +	127
	20	14,400	4,100 +	140	12,500	2,200 +	121	14,300	4,000 +	139
5	37	710,000		100	440,000	270,000	62	370,000	340,000 -	52
	30	980,000	270,000 +	138	830,000	150,000 +	118	770,000	60,000 +	108
	20	920,000	210,000 +	130	970,000	260,000 +	137	1,060,000	350,000 +	149
6	37	14,100		100	14,500	400 +	103	15,900	1,800 +	113
	30	18,600	4,500 +	132	15,900	1,800 +	113	16,300	2,200 +	114
	20	18,000	3,900 +	128	15,700	1,600 +	111	16,100	2,000 +	116
7	37	2,400,000		100	1,740,000	660,000 -	72	2,290,000	110,000 -	97
	30	2,950,000	550,000 +	123	3,150,000	750,000 +	131	3,190,000	790,000 +	133
	20	3,060,000	660,000 +	127	3,120,000	720,000 +	130	2,960,000	560,000 +	123
8	37	17,300		100	18,100	6,300 +	153	18,300	6,500 +	155
	30	31,200	7,900 +	343	32,800	20,600	320	36,200	24,900 +	507
	20	39,600	27,800 +	466	35,400	13,200	302	35,700	23,900 +	303

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	95												
	89												
	95												
	113												
	103												
11	93												
	92												
	71												
12	90												
	139												
	135												
13	99												
	118												
	112												
14	104												
	155												
	143												
15	110												
	101												
	96												
16	99												
	140												
	122												
17	84												
	94												
	97												

TABLE 1 (*continued*)

Sample	Temperature °C	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
18	37	960,000		100	1,280,000	320,000 +	133	990,000	30,000 +	103
	30	1,100,000	140,000 +	115	1,220,000	260,000 +	127	1,240,000	280,000 +	129
	20	1,090,000	130,000 +	114	1,390,000	430,000 +	145	1,240,000	280,000 +	129
19	37	154,800		100	135,600	19,200	88	148,100	6,700 −	96
	30	185,400	30,600 +	120	142,800	12,200	92	120,300	34,500 −	78
	20	182,600	27,800 +	118	122,800	32,000	79	178,700	23,900 +	115
20	37	660,000		100	660,000		100	810,000	150,000 +	123
	30	720,000	60,000 +	109	600,000	60,000	91	820,000	160,000 +	124
	20	870,000	210,000 +	132	800,000	140,000 +	121	860,000	200,000 +	130
21	37	2,100		100	2,500	400 +	119	2,200	100 +	105
	30	2,600	500 +	124	2,100		100	2,400	300 +	113
	20	2,500	400 +	119	2,700	600 +	129	3,400	1,300 +	162
22	37	8,000		100	12,000	4,000 +	150	18,000	10,000 +	225
	30	34,000	26,000 +	425	32,000	24,000 +	400	35,000	27,000 +	437
	20	16,000	8,000 +	200	32,000	24,000 +	400	36,000	28,000 +	450
23	37	2,000		100	3,000	1,000 +	150	1,000	1,000 —	50
	30	6,000	4,000 +	300	2,000		100	3,000	1,000 +	150
	20	4,000	2,000 +	200	1,000	2,000 +	200	1,000	1,000 —	50
24	37	73,000		100	59,000	14,000 −	81	35,000	38,000 —	48
	30	76,000	3,000 +	104	93,000	20,000 +	128	66,000	7,000 —	90
	20	29,000	44,000 −	40	11,000	62,000 −	15	15,000	58,000 —	20
		1,240,000		100	1,687,000	447,000 +	140	1,150,000	50,000 −	96
	30	2,284,000	1,044,000 +	190	2,304,000	1,064,000 +	192	1,181,000	19,000	98
	20	365,000	875,000 −	27	19,000	1,181,000 −	2	2,003,000	803,000 +	167

28	35°	72,000		100	747,000	675,000 +	1,037	1,290,000	1,458,000 +	1,792		
	30°	270,000	2,000	65	621,000	324,000 -	904	1,428,000	1,566,000 +	2,052		
	20°	192,000	10,000	57	51,000	11,000	13	21,000	51,000	30		
27	35°	648,000		100	12,000	18,000	30	17,000	13,000 -	78		
	30°	387,000	327,000 -	645	321,000	321,000 +	625	311,000	281,000 +	368		
	20°	558,000	276,000 -	597	502,000	142,000 +	857	345,000	285,000 +	575		
28	35°	90,000		100	76,000	4,000 -	95	105,000	25,000 +	131		
	30°	134,000	54,000 -	167	125,000	45,000 +	156	130,000	50,000 +	162		
	20°	157,000	47,000 +	159	98,000	18,000 +	122	151,000	71,000 +	189		
29	35°	102,000		100	164,000	62,000 +	161	243,000	141,000 +	238		
	30°	160,000	58,000 +	157	174,000	72,000 +	171	210,000	108,000 +	206		
	20°	215,000	113,000 +	211	184,000	82,000 +	149	175,000	73,000 +	171		
30	35°	3,050,000		100	3,290,000	660,000	84	2,860,000	1,090,000 —	72		
	30°	6,740,000	4,790,000 +	170	6,230,000	2,330,000 +	159	4,170,000	220,000 +	105		
	20°	7,290,000	4,810,000 +	184	6,160,000	2,510,000 +	163	650,000	3,300,000 —	16		
31	35°	520,000		100	670,000	150,000 +	129	1,050,000	330,000 +	202		
	30°	1,780,000	1,440,000 +	381	1,800,000	720,000 +	336	2,780,000	2,260,000 +	534		
	20°	1,980,000	1,140,000 +	323	1,680,000	1,160,000 +	323	1,660,000	1,110,000 +	319		
32	35°	250,000		100	170,000	80,000	68	350,000	100,000 +	140		
	30°	580,000	330,000 +	232	630,000	380,000 +	252	520,000	270,000 +	208		
	20°	630,000	380,000 +	252	520,000	270,000 +	208	410,000	160,000 +	164		
33	35°	19,000		100	16,000	3,000	84	4,000	15,000 —	21		
	30°	39,000	20,000 +	205	43,000	21,000 +	226	30,000	11,000 +	158		
	20°	36,000	17,000 +	189	27,000	5,000 +	142	28,000	9,000 +	147		
34	35°	90,000		100	98,000	18,000 +	122	74,000	6,000 —	92		
	30°	114,000	34,000 +	142	122,000	42,000 +	152	110,000	30,000 +	137		
	20°	87,000	3,000 +	106	123,000	43,000 +	154	97,000	17,000 +	121		

TABLE I—*continued*

Sample	Temperature C	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
35	37°	106,300		100	125,200	18,900 +	118	131,300	25,000 +	124
	30°	138,100	31,800 +	130	145,200	38,900 +	137	111,900	5,600 +	107
	20°	133,100	26,800 +	125 +	116,100	10,000 +	109	91,900	11,400 −	89
36	37	30,000		100	390,000	360,000 +	1,300	240,000	210,000 +	800
	30	90,000	60,000 +	300	40,000	10,000 +	133	620,000	590,000 +	2,067
	20	60,000	30,000 +	200	30,000		100	320,000	290,000 +	1,067
37	37	10,000		100	10,000		100	70,000	60,000 +	700
	30	50,000	40,000 +	500	10,000		100	800,000	790,000 +	8,000
	20	40,000	30,000 +	400	30,000	20,000 +	300	610,000	600,000 +	6,100
38	37	20,000		100	20,000		100	270,000	250,000 +	1,350
	30	30,000	10,000 +	150	20,000		100	590,000	570,000 +	2,950
	20	30,000	10,000 +	150	30,000	10,000 +	150	380,000	360,000 +	1,900
39	37	20,000		100	40,000	20,000 +	200	140,000	120,000 +	700
	30	60,000	40,000 +	300	20,000		100	260,000	240,000 +	1,300
	20	20,000		100	40,000	20,000 +	200	300,000	280,000 +	1,500
40	37°	10,000		100	10,000		100	60,000	50,000 +	600
	30°	10,000		100	10,000		100	650,000	640,000 +	6,500
	20°	10,000		100	10,000		100	40,000	30,000 +	400
41	37°	20,000		100	20,000		100	150,000	130,000 +	750
	30°	30,000	10,000 +	150	20,000		100	190,000	170,000 +	950
	20°	10,000	10,000	50	20,000		100	19,000	1,000 −	95
42	37°	510,000		100	250,000	250,000	49	420,000	90,000 −	83
	[illegible]	[illegible]	[illegible]	94	530,000	40,000 +	107	650,000	110,000 +	127
	20	480,000	30,000	94	540,000	50,000 +	106	800,000	290,000 +	157

43											
45											
46											
47											
48											
49											
50											
51											

TABLE I—*Continued.*

Sample	Temperature °C	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
52	37°	75,000		100	64,000	11,000	85	143,000	68,000+	191
	30°	153,000	78,000+	204	171,000	96,000+	228	175,000	100,000+	233
	20°	149,000	74,000+	199	170,000	95,000+	227	197,000	122,000+	263
53	37°	86,000		100	93,000	7,000	108	172,000	86,000+	200
	30°	143,000	57,000+	166	121,000	35,000+	141	120,000	34,000+	140
	20°	134,000	48,000+	156	106,000	20,000+	123	113,000	27,000+	131
54	37°	87,000		100	345,000	263,000+	4[illegible]	369,000	287,000+	450
	30°	69,000	13,000	84	396,000	311,000	483	368,000	286,000+	449
	20°	76,000	6,000-	93	137,000	55,000+	167	213,000	131,000+	260
55	37°	6,000		100	1,000	5,000-	17	16,000	10,000+	267
	30°	26,000	20,000+	433	9,000	3,000+	150	18,000	12,000+	300
	20°	8,000	2,000+	133	7,000	1,000+	117	8,000	2,000+	133
56	37°	26,000		100	71,000	45,000+	273	73,000	47,000+	280
	30°	691,000	665,000+	2,658	880,000	804,000+	3,192	671,000	645,000+	2,581
	20°	458,000	432,000+	1,762	677,000	651,000+	2,604	197,000	171,000+	1,912
57	37°	102,000		100	13,000	89,000-	12	69,000	33,000—	68
	30°	816,000	714,000+	800	867,000	865,000+	948	697,000	595,000+	683
	20°	1,159,000	1,057,000+	1,136	1,465,000	1,263,000+	1,338	1,653,000	1,551,000+	1,620
58	37°	110,000		100	252,000	142,000+	229	146,000	36,000+	133
	30°	163,000	53,000+	148	341,000	231,000+	310	174,000	64,000+	158
	20°	194,000	84,000+	176	178,000	68,000+	162	110,000		100
59	37°	5,000		100	170,000	114,000+	304	357,000	201,000+	637
	[illegible]	[illegible]	[illegible]	[illegible]	39,000	18,000+	1[illegible]	235,000	179,000	120
	20°	[illegible]	[illegible]	[illegible]	140,000	100,000	379	92,000	36,000+	164

	30°	26,000	13,000+	200	40,000	6,000	146	71,000	58,000+	546
	20°	20,000	7,000+	154	20,000	7,000	154	37,000	24,000	285
	37°	8,000		100	7,000	1,000	87	168,000	160,000+	2,100
	30°	18,000	10,000+	225	11,000	3,000+	137	106,000	98,000+	1,325
	20°	12,000	1,000—	150	11,000	3,000+	137	58,000	50,000+	725
62	37°	6,000		100	6,000		100	6,000		100
	30°	12,000	6,000+	200	8,000	2,000+	133	8,000	2,000+	133
	20°	7,000	1,000—	116	6,000		100	9,000	3,000+	150
63	37°	28,000		100	15,000	13,000	54	28,000		100
	30°	31,000	3,000+	111	25,000	3,000	89	41,000	13,000+	146
	20°	20,000	8,000	71	31,000	7,000	75	22,000	6,000—	79
64	37°	45,000		100	39,000	6,000	87	50,000	5,000+	111
	30°	42,000	3,000+	93	63,000	18,000+	140	70,000	25,000+	155
	20°	30,000	15,000+	67	48,000	3,000+	107	36,000	9,000—	80
65	37°	22,000		100	12,000	10,000	55	21,000	1,000—	95
	30°	33,000	11,000+	150	30,000	8,000+	136	17,000	5,000—	77
	20°	23,000	1,000+	105	18,000	4,000	82	36,000	14,000+	164
66	37°	490,000		100	371,000	119,000	76	795,000	305,000+	162
	30°	1,405,000	915,000+	286	525,000	35,000+	107	459,000	31,000—	94
	20°	767	489,233	0·1	1,123	488,877	0·2	1,308	488,692—	0·2
67	37°	76,000		100	95,000	19,000+	126	83,000	7,000+	109
	30°	69,000	7,000—	91	87,000	11,000+	114	96,000	20,000+	126
	20°	86,000	10,000+	113	60,000	16,000	79	50,000	26,000—	66
68	37°	6,000		100	3,000	3,000	50	3,000	3,000—	50
	30°	290,000	284,000+	4,833	100,000	94,000+	1,666	180,000	174,000+	3,000
	20°	330,000	324,000+	5,500	360,000	354,000+	6,000	470,000	464,000+	7,833

TABLE I (continued)

Sample	Temperature C	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
69	37	51,000		100	56,000	5,000 +	110	58,000	7,000 +	114
	30	123,000	72,000 +	241	99,000	18,000 +	194	105,000	54,000 +	206
	20	99,000	48,000 +	194	63,000	12,000 +	124	66,000	15,000 +	129
70	37	25,000		100	30,000	5,000 +	120	30,000	5,000 +	120
	30	174,000	149,000 +	696	146,000	121,000 +	584	124,000	99,000 +	496
	20	177,000	152,000 +	708	125,000	100,000 +	500	131,000	106,000 +	524
71	37	87,000		100	120,000	33,000 +	138	157,000	70,000 +	180
	30	380,000	293,000 +	437	338,000	251,000 +	389	322,000	235,000 +	370
	20	407,000	320,000 +	469	350,000	263,000 +	402	358,000	271,000 +	411
72	37	7,000		100	3,000	4,000	43	2,000	5,000—	29
	30	13,000	6,000 +	186	15,000	8,000 +	214	7,000		100
	20	2,000	5,000	29	5,000	2,000	71	5,000	2,000—	71
73	37	8,000		100	6,000	2,000	75	6,000	2,000—	75
	30	12,000	4,000 +	150	10,000	2,000 +	125	8,000		100
	20	8,000		100	8,000		100	7,000	1,000—	87
74	37	14,000		100	12,000	2,000	86	8,000	6,000—	57
	30	28,000	14,000 +	200	27,000	13,000 +	193	17,000	3,000+	121
	20	21,000	7,000 +	150	14,000		100	20,000	6,000+	142
75	37	3,000		100	1,000	2,000	33	1,000	1,000+	133
	30	6,000	3,000+	200	5,000	2,000 +	167	3,000	....	100
	20	3,000		100	2,000	1,000	67	1,000	2,000—	33
				100	23,000	5,000	82	25,000	3,000	89

| | | |

TABLE 1 *(continued)*

Sample	Temperature C°	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
86	37°	5,000		100	6,000	1,000+	120	17,000	12,000+	340
	30°	8,000	3,000+	160	7,000	2,000+	140	16,000	11,000+	320
	20°	10,000	5,000+	200	7,000	2,000+	140	27,000	22,000+	540
87	37°	27,000		100	15,000	12,000	56	34,000	7,000+	126
	30°	191,000	164,000+	707	171,000	144,000+	633	138,000	111,000+	511
	20°	229,000	202,000+	848	161,000	134,000+	596	129,000	102,000+	478
88	37°	41,000		100	32,000	9,000	78	59,000	18,000+	144
	30°	319,000	278,000+	778	346,000	289,000+	829	498,000	457,000+	1,215
	20°	512,000	471,000+	1,249	774,000	733,000+	1,888	751,000	710,000+	1,832
89	37°	6,000		100	9,000	3,000+	150	10,000	4,000+	167
	30°	39,000	33,000+	583	40,000	34,000+	667	87,000	81,000+	1,450
	20°	56,000	50,000+	933	44,000	38,000+	733	44,000	38,000+	733
90	37°	401,000		100	468,000	67,000+	117	467,000	66,000+	116
	30°	6,000	395,000—	1	6,000	395,000—	1	19,000	382,000—	5
	20°	8,000	393,000—	2	10,000	391,000—	2	17,000	384,000—	4
91	37°	609,000		100	731,000	142,000+	123	572,000	37,000—	94
	30°	2,497,000	1,888,000+	410	1,544,000	935,000+	253	937,000	328,000+	154
	20°	4,019,000	3,410,000+	660	5,660,000	5,051,000+	929	4,238,000	3,629,000+	696
92	37°	331,000		100	382,000	51,000+	115	398,000	67,000+	120
	30°	434,000	103,000+	131	409,000	78,000+	124	424,000	93,000+	128
	20°	420,000	89,000+	127	357,000	26,000+	108	477,000	146,000+	144
[illegible]	37°	328,000		100	282,000	46,000	86	247,000	81,000	75
	30°	344,000	16,000+	105	257,000	71,000	78	378,000	50,000+	115
	20°	330,000	2,000+	101	336,000	8,000+	102	351,000	24,000+	107

94	37°	27,000		100	23,000	4,000—	85	81,000	54,000+	341
	30°	56,000	29,000+	207	55,000	28,000+	204	83,000	56,000+	307
	20°	60,000	33,000+	222	63,000	36,000+	233	106,000	79,000+	393
95	37°	374,000		100	325,000	49,000—	87	319,000	55,000—	86
	30°	522,000	148,000+	140	518,000	144,000+	138	504,000	130,000+	135
	20°	511,000	137,000+	137	561,000	187,000+	150	425,000	51,000+	114
96	37°	30,000		100	30,000		100	290,000	260,000+	967
	30°	30,000		100	10,000	20,000—	33	100,000	70,000+	333
	20°	3,000	27,000—	10	3,000	27,000—	10	3,000	27,000—	10
97	37°	40,000		100	130,000	90,000+	325	30,000	10,000—	75
	30°	20,000	20,000—	50	6,000	34,000—	15	100,000	60,000+	250
	20°	6,000	34,000—	15	3,000	37,000—	7	3,000	37,000—	7
98	37°	30,000		100	200,000	170,000+	667	3,980,000	3,950,000+	13,267
	30°	40,000	10,000+	133	40,000	10,000+	133	790,000	760,000+	2,633
	20°	20,000	10,000—	67	20,000	10,000—	67	100,000	70,000+	333
99	37°	33,000		100	55,000	22,000+	167	67,000	34,000+	203
	30°	33,000		100	55,000	22,000+	167	102,000	69,000+	309
	20°	49,000	16,000+	148	59,000	26,000+	179	66,000	33,000+	200
100	37°	20,000		100	10,000	10,000—	50	100,000	80,000+	500
	30°	30,000	10,000+	150	30,000	10,000+	150	190,000	170,000+	950
	20°	40,000	20,000+	200	40,000	20,000+	200	310,000	290,000+	1,550

TABLE 2. SUMMARY OF HIGHEST AND LOWEST COUNTS FOUND ON EACH COMBINATION OF INCUBATION TEMPERATURE AND MEDIUM

Medium, and incubation temperature (C.)	Counts expressed as per cent	Total number of highest counts	Number of counts up to 200 per cent	Number of counts up to 500 per cent	Number of counts up to 1000 per cent	Number of counts up to 5000 per cent	Number of counts up to 10,000 per cent	Total number of lowest counts[a]
Plain 37°	100.0	0	0	0	0	0	0	4
Lactose 37°	175.3	2	1	0	0	0	0	7
Dextrose 37°	444.9	10	6	4	2	1	1	16
Plain 30°	519.1	17	11	1	1	1	1	2
Lactose 30°	453.5	11	9	2	2	0	0	2
Dextrose 30°	778.6	22	17	11	4	2	0	1
Plain 20°	411.4	12	3	2	0	0	0	4
Lactose 20°	498.5	5	3	3	1	0	0	3
Dextrose 20°	664.8	21	13	6	3	1	0	3
Total		100	63	29	13	5	2	

[a] Twenty samples [illegible] the combination of temperature and medium gave [illegible] counts [illegible]

The results given in table 1 may be compared in several ways to show the variation obtained from each medium and incubation temperature. The writers have preferred to make comparisons on the basis of the number of highest and lowest counts found under each condition and also to compare the average percentage variation in count of all samples, regarding the 37° count on plain agar as 100 per cent. These comparisons are given in table 2, in which the outstanding features are as follows: (1) from all samples, higher counts were obtained from some other medium and temperature combination than the 37° count on plain agar; (2) of these higher counts, 63 per cent were increased twofold, 29 per cent fivefold, 13 per cent tenfold, 5 per cent fiftyfold, and 2 per cent more than a hundredfold.

Comparing the effects of incubation temperatures on all media, it was found that 50 per cent of the highest counts were obtained at 30°, 38 per cent at 20°, and 12 per cent at 37°. Of the lowest counts recorded, 6.2 per cent were obtained at 30°, 16.2 per cent at 20°, and 77.6 per cent at 37°.

The results of the various compositions of media compared at all temperatures showed that 29 per cent of the highest counts were obtained on plain agar, 18 per cent on lactose agar, and 53 per cent on dextrose agar. Of the lowest counts recorded, 33.7 per cent were obtained on plain agar, 46.2 per cent on lactose agar, and 20.1 per cent on dextrose agar. On the basis of the 37° plain-agar count, the counts for all samples, as represented by the average percentage figures, show variations ranging from less than a twofold increase, for lactose agar at 37°, to more than a sevenfold increase, for dextrose agar at 30°.

From these data it appears that dextrose agar at 30° or 20° has distinct advantages over any of the other combinations used, for obtaining higher counts. There is comparatively little choice between plain agar at 20° and 30°, and lactose agar at the same temperatures, altho plain agar at 30° seems to have a slight advantage in the number of highest counts and the average percentage increase. The 37° counts on all of the media are decidedly unfavorable in comparison with those of the other incubation temperatures. Dextrose agar, however, has evident advantages over plain and lactose agar at this temperature. The slight difference which is found between the two latter media at 37° is in favor of the lactose agar.

Variation in counts at 37° C.

While lower bacteria counts were found at 37° than at the lower incubation temperatures, it is recognized that longer incubation periods are necessary in order to develop higher counts at the lower temperatures. At the end of forty-eight hours, the 37° counts have frequently proved higher than those resulting from similar incubation periods at the lower temperatures. An additional incubation period of two or three days, however, has always been necessary in order to develop the higher counts at these lower temperatures. On the other hand, there is usually very little increase in the 37° count after the first forty-eight-hour period. These facts might easily be interpreted to mean that forty-eight hours at 37° represents a time-temperature relationship which cannot be reduced if the greatest growth in the shortest period of time is desired. This particular temperature and incubation period may therefore be looked upon as the minimum and cannot be changed without materially affecting the usefulness of the results. The exacting demands for inspection work, which have determined the use of the 37° forty-eight-hour count, are not

operative in research work, in which the longer incubation periods and lower temperatures are generally used. These longer incubation periods at lower temperatures are used for the purpose of obtaining maximum counts where immediate results are not essential. Since this is the main object, greater variations in time or temperature may be used without affecting the results to the same degree that they would be affected by similar variations in the 37° forty-eight-hour counts.

Recognizing the importance of maintaining the correct temperature for the 37° count, an attempt was made to find out what variations in counts would result from possible differences of temperature due to piling the individual plates in a compact mass, as compared with the results obtained by so arranging the plates as to allow free circulation of air around each one. The former condition occasionally exists in any laboratory, particularly when a large number of plates must be incubated at the same time. In these experiments, the capacity of the incubator was only about half utilized. The sources of heat in the incubator were at the bottom, two and one-half inches below the temporary floor, at the top, and on two sides. Variations in temperature to which individual plates might be exposed, therefore, would be due to the slow diffusion of the heat resulting from the diminished ventilation around the piles of plates.

For these comparisons, two samples of market milk containing approximately the same number of bacteria, and with no apparent difference in the flora, were selected. A sufficient volume of a single dilution was made so that about 200 plates could be prepared from the same bottle. The samples were diluted with the object of obtaining between 30 and 100 colonies to the plate. All plates were poured from the same batch of plain agar. They were placed in the incubator so that consecutive numbers would lie next to each other. The average of the counts from plates bearing two consecutive numbers was considered as the count for a single sample.

In testing the effect of the free circulation of air during incubation, 200 plates were arranged in layers on wire screens with about one-half inch air space between each layer. The bottom layer was one and one-half inches from the floor of the incubator. A uniform temperature of 37° at two inches from the top, and the usual ventilation of the incubator were maintained throughout the forty-eight-hour period. The counts obtained from these samples are shown in table 3.

TABLE 3.—BACTERIA COUNTS OBTAINED FROM 100 SAMPLES OF THE SAME MILK WHEN AIR HAD CIRCULATED FREELY AROUND EACH PLATE DURING INCUBATION

Sample	Bacteria per cubic centimeter	Sample	Bacteria per cubic centimeter
1	240,000	51	225,000
2	235,000	52	240,000
3	250,000	53	255,000
4	250,000	54	185,000
5	285,000	55	240,000
6	315,000	56	365,000
7	270,000	57	245,000
8	200,000	58	265,000
9	260,000	59	245,000
10	280,000	60	150,000
11	235,000	61	230,000
12	260,000	62	215,000
13	200,000	63	305,000
14	170,000	64	245,000
15	225,000	65	175,000
16	190,000	66	275,000
17	345,000	67	195,000
18	215,000	68	275,000
19	260,000	69	275,000
20	155,000	70	275,000
21	205,000	71	245,000
22	200,000	72	145,000
23	270,000	73	275,000
24	160,000	74	115,000
25	240,000	75	205,000
26	185,000	76	240,000
27	225,000	77	170,000
28	300,000	78	340,000
29	285,000	79	215,000
30	275,000	80	225,000
31	295,000	81	210,000
32	195,000	82	255,000
33	290,000	83	275,000
34	195,000	84	270,000
35	215,000	85	255,000
36	305,000	86	270,000
37	245,000	87	195,000
38	300,000	88	125,000
39	210,000	89	270,000
40	270,000	90	225,000
41	280,000	91	200,000
42	295,000	92	200,000
43	155,000	93	220,000
44	250,000	94	315,000
45	205,000	95	210,000
46	280,000	96	230,000
47	180,000	97	200,000
48	205,000	98	250,000
49	205,000	99	270,000
50	155,000	100	350,000

In testing the effect of piled plates, the procedure was as follows: Piles of 12 plates each were arranged in a solid block, 6 piles long and 3 piles wide, and containing, in all, 216 plates. The same uniformity of temperature at two inches from the top, and the same ventilation, were maintained in the incubator as in the first experiment. Likewise, the average of the counts of two adjacent plates in each pile was taken as the count for a single sample. The two bottom plates in each pile are not included in the results, as it was desirable to consider only the counts from the plates kept at the same distance from the bottom of the incubator as were those in the first experiment; therefore the results are given for only five samples to the pile. In table 4, which is constructed to show the relative position of each pile in the block, appear the results obtained for each sample, that is, the average of each two adjacent plates.

TABLE 4. BACTERIA COUNTS OBTAINED FROM SAMPLES OF THE SAME MILK WHEN PLATES WERE PILED IN A SOLID BLOCK DURING INCUBATION

Pile 1	Pile 2	Pile 3	Pile 4	Pile 5	Pile 6
424,000	402,000	366,000	348,000	404,000	456,000
419,000	346,000	336,000	403,000	358,000	366,000
419,000	305,000	303,000	379,000	402,000	307,000
368,000	367,000	272,000	345,000	360,000	364,000
328,000	308,000	240,000	191,000	152,000	302,000
Average 392,000	364,000	297,000	323,000	335,000	359,000

Pile 7	Pile 8	Pile 9	Pile 10	Pile 11	Pile 12
400,000	364,000	340,000	319,000	307,000	331,000
369,000	316,000	235,000	313,000	318,000	306,000
363,000	273,000	79,000	245,000	290,000	348,000
354,000	157,000	35,000	126,000	33,000	273,000
350,000	15,000	7,000	9,000	11,000	300,000
Average 373,000	245,000	143,000	202,000	192,000	312,000

Pile 13	Pile 14	Pile 15	Pile 16	Pile 17	Pile 18
400,000	344,000	403,000	361,000	457,000	341,000
350,000	376,000	363,000	397,000	401,000	311,000
375,000	240,000	371,000	342,000	302,000	308,000
350,000	371,000	295,000	283,000	291,000	315,000
300,000	286,000	247,000	211,000	309,000	280,000
Average 355,000	339,000	334,000	319,000	294,000	311,000

The results given in tables 3 and 4 show some striking facts concerning ne effect upon the counts of these two different methods of exposure the plates to the uniform conditions of temperature and ventilation aintained in the incubator. In table 4 there is a marked difference the results from all top samples and samples in the corner piles, as mpared with those from the bottom of the piles and particularly from ose at the bottom of the piles on the inside of the block. In order to ow these variations in counts, the standard deviation, the coefficient f variability, and the probable error were calculated for the entire number f samples in each set and for certain groups of samples which were packed the solid block. These mathematical expressions are shown in table 5.

ABLE 5. VARIATIONS IN COUNTS DUE TO METHODS OF PILING PLATES AS SHOWN BY COEFFICIENT OF VARIABILITY, STANDARD DEVIATION, AND PROBABLE ERROR

Samples used for calculations	Number of samples	Average count	Standard deviation	Probable error	Coefficient of variability per cent
ir space between all plates table 3	100	237,350*	± 49,014*	33,059*	20 6
Plates in solid block, all samples table 4	90	307,000	± 105,000	70,822	34 2
Samples in corner piles only Nos 1, 6, 13, 18	20	368,000	± 45,485	30,679	12 3
Samples in side piles only (Nos 2, 3, 4, 5, 7, 12, 14, 15, 16, 17	50	330,000	± 64,000	43,168	19 4
Samples in center piles only (Nos 8, 9, 10, 11)	20	195,000	± 138,016	91,742	69 7
Samples from top plates of each pile	18	365,000	± 39,200	26,440	10 7
Samples from bottom plates of each pile	18	201,000	± 123,200	83,098	61 3

* Not to be compared with corresponding figures from samples shown in the remainder of the table because of the variation in bacterial content of the milk

The significant figures in table 5 are those representing the coefficient of variability although the other figures contribute toward a more comprehensive understanding of the variations found in the different groups of samples. The coefficient of variability obtained from samples when a free circulation of air was allowed between the plates was 20.6 per cent; whereas this

variability was increased to 34.2 per cent from samples that were piled in a solid block. This variation of 34.2 per cent is the resultant of larger and smaller variations from compound groups of the entire block of plates. The coefficients of variability of 10.7 per cent and 12.3 per cent from samples on the tops of all piles and from all plates in the corner piles, respectively, when compared with the higher coefficients of variability of 19.4 per cent, 69.7 per cent, and 61.3 per cent from those samples in positions less favorably situated, certainly indicate an important consideration in judging the reliability of the 37° count.

In order to determine to what extent variations in temperature within the solid block of plates were responsible for discrepant counts, an attempt was made to obtain temperature records at different places in the pile with a recording thermometer. In the absence of a more delicate apparatus, temperatures were determined with a Tycos recording instrument. All necessary precautions were observed in order to duplicate the normal temperature conditions from which the foregoing counts were obtained. These records, showing the temperature for each hour until the desired temperature of 37° was reached, are shown in table 6. Determination 1 is made from the empty incubator at a point midway between the top and the bottom; determination 2 was made under the same conditions except that the bulb of the thermometer was placed inside a petri plate; determination 3 was obtained with the bulb inside the fifth plate from the bottom of a single pile of 12 plates; determination 4 was the result of having the bulb inside the fifth plate from the bottom of a pile corresponding to pile 13 in the block of plates shown in table 4; determinations 5 and 6 were produced from plates in the same position in piles corresponding to numbers 15 and 8, respectively, of the same table. The vertical distance from the top of the incubator to the plate containing the thermometer bulb is the same as that to one of the plates included in determining the average count of the fourth ample from the top.

TABLE 6 TEMPERATURES RECORDED EACH HOUR AT DIFFERENT PLACES IN A BLOCK OF TIGHTLY PACKED PETRI PLATES

(In degrees centigrade)

Determination	Temperature at start	Temperatures recorded after								
		1 hour	2 hours	3 hours	4 hours	5 hours	6 hours	7 hours	8 hours	9 hours
1	20 0°	35 0°	37 0	.	.	.	.			.
2	20 5°	35 5°	37 0°							.
3	20 5°	31 0°	34 4°	36 0°	37 0°					.
4	21 5°	29 4°	33 8°	35 5°	36 6°	37 0°				.
5	21 0°	27 0°	31 6°	33 8°	35 0°	35 5°	35 5°	36 0°	36 6°	37 0°
6	21 0°	25 0°	28 0°	31 0°	32 7°	34 4°	35 5°	35 5°	36 0°	37 0°

The temperature records clearly indicate the relative length of time required by plates in different positions to reach the normal temperature. If records from inside the block of plates could have been obtained readily, it is quite probable that the length of time necessary to reach 37° would have proved even greater than that shown by determination 6. The rapidity of the heat diffusion apparently did not suffice to heat the entire block of plates soon enough to prevent marked irregularities in the counts made from the inner piles of the block. This fact emphasizes the greater likelihood of discrepant results from overcrowded incubators, or from other causes which in any way reduce the ventilation around the interior plates. In the positions represented by determinations 5 and 6, the temperatures were below normal for nine hours. This period, during which the plates in these positions were below normal, amounts to approximately 19 per cent of the entire incubation period. Plates on the outside of the pile, however, remained below normal temperature for a much shorter period, and consequently their counts were much higher and more nearly uniform than those obtained from plates that had not been maintained at the normal temperature for the entire period.

Discussion

The wide range of variations in the counts obtained by different incubation temperatures and media emphasizes the inadequacies of any single combination of temperature and media for determining the maximum

bacteria counts from miscellaneous samples of milk. Plain agar at 37° for forty-eight hours is unquestionably the least favorable combination for this purpose; the use of lactose agar at this temperature appears to have few, if any, advantages over plain agar; and altho dextrose agar at 37° has distinct advantages over those media, nevertheless the majority of the results obtained from it are lower than those produced at 20° or 30° for five days.

For developing the maximum counts, dextrose agar at 30° for five days seems to be superior to any of the other combinations considered in this paper. This medium at 20° for five days is also preferable to plain or lactose agar at either 30° or 20°. The same lack of a distinct superiority of one of these latter two media over the other exists at the lower temperatures, as well as at 37°.

Counts obtained at 37° after forty-eight hours are probably subject to greater discrepancies than those obtained at the lower temperatures for longer periods of time. It has been shown that the normal variations in temperature thruout a mass of tightly packed plates is sufficient to cause as high as a fivefold variation from the same sample of milk; whereas only a threefold variation was found when the plates were arranged to allow a free circulation of air around each one. To avoid gross discrepancies, it is necessary, on the basis of the previous results, to provide such ventilation in 37° incubators as will heat each individual plate in a block at an approximately equal rate.

Possible variations in bacteria counts resulting from the present plate method of enumeration should not be considered as a condition eliminating their usefulness. Bacteria counts, together with the discrepancies to which they are subject, should be considered only with full knowledge of their limitations and of the fact that they constitute but one item of the evidence necessary to grade milk into distinct classes according to its wholesomeness and keeping quality.

In order to harmonize these variations with existing numerical bacterial standards, it is essential that all factors tending to cause variations and discrepancies be reduced to a minimum. Furthermore, results obtained from such manipulations, even tho necessitating the statement of fixed numbers, should be interpreted in a manner which recognizes the lack of intrinsic value of these numbers for denoting such exact degrees of bacterial quality as the statement of fixed numerical expressions implies.

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GUST, 1921 MEMOIR 44

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA

BENJAMIN P. YOUNG

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA

ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA[1]

BENJAMIN P. YOUNG

Many excellent studies have been made by various investigators on the morphology of the thoracic sclerites of different groups of insects. A number of these investigators have covered the entire class Insecta with the hope of determining the ground plan on which a typical thoracic segment is based. Such investigators have done much toward establishing a uniform terminology for this particular part of insect anatomy. Other workers have limited themselves to the consideration of a smaller group, as the order or the family. But in no place in the literature has the writer been able to find a record of extensive studies on the order Diptera. Snodgrass (1909, a and b) and Crampton (1909) have each figured two species; others have made even briefer references to the group. As for comprehensive work on the relation of the anterior abdominal sclerites to those of the metathorax, nothing has been found, isolated text figures being the only contributions along this line.

Through this study, which had as its primary aim the homologizing of the abdominal and thoracic sclerites in species of each available family of the Diptera, it was hoped that something might be added to the morphological literature of the group. Among the indices to phylogeny, wing venation has come to be regarded as one of the most valuable because it is the most evident; the morphology of the genitalia has not been used as much because of the difficulties attending such studies, but at present it is gaining favor because of the desirability of using all available means in throwing light on the above-mentioned problem. Vestiture has been made use of, especially by dipterologists, but mostly for generic and specific characters. If the external morphology of this particular part of the exoskeleton can contribute but its share toward the history of the descent of the group, the writer will feel that his efforts have not been in vain.

Furthermore, systematists of the order are not in accord as to the

[1] This investigation was suggested by, and carried on under the direction and supervision of, Dr. O. A. Johannsen, to whom the writer is indebted not only for many suggestions growing out of his experience with the Diptera as a whole, but also for his sincere interest shown throughout the progress of

number of abdominal segments in different families. Some have counted only definitive segments and used such for key characters, while others have taken into consideration the true number as indicated by the spiracles. One of the reasons for figuring herein the pleurites of the meso- and the metathorax and the sclerites of the proximal abdominal segments of some of the commoner species of fifty-seven families of this order, is to aid in bringing about uniformity in interpretation.

Having studied but a few species of each family, the writer cannot say that the characters of the one figure hold throughout the family, but nevertheless a typical species should afford external facies more or less characteristic of the family.

METHODS AND TECHNIQUE

Practically all of this study was made from dried specimens which had been soaked for from three hours to seven days in a 10-per-cent solution of potassium hydroxide. Some forms were already clear enough for study but were allowed to remain in the clearer for a few hours in order to clear them sufficiently for study and handling. The specimens were then washed in distilled water to which a few drops of acetic acid had been added, and preserved in 70-per-cent alcohol.

It was soon found impossible to see sutures in some forms, especially the smaller species, without dissection, and it was only after each form had been halved by a median longitudinal cut with a scalpel that the work progressed with dispatch. This operation, which was done under 70-per-cent alcohol, was followed by the removal of the viscera of each half, but during the latter operation close attention was given also to the tracheal branches leading to the spiracles in order to learn the position and number of these in the abdomen. The left half was then available for external study, while the right was reserved for internal study of phragmas, apodemes, and apophyses as an aid to the more definite location of sclerites.

The binocular microscope was used both in making dissections and for the study of specimens in 70-per-cent alcohol. Drawings were made on coordinate paper with the aid of an ocular micrometer laid off in squares. To insure the object's remaining in the same place, a small piece of plasticine, used in modeling, was stuck to the bottom of a watch glass and the fly was held against the bottom of the glass by means of two bent pins

stuck into the plasticine just above each end of the insect. For drawings requiring two or three hours this proved to be a very satisfactory method, as the alcohol remains clear for that length of time.

In each drawing an attempt was made to show all chitinized areas clear and all membranes stippled. There are sclerites to be found, however, in which it is difficult to class the integument as either chitinous or membranous. Assuming the membranous state to be the more primitive, increasing amounts of chitin laid down in membrane were represented by a decreasing amount of stippling, that is, by placing the dots farther and farther apart. All outlines, as well as sutures (using the term in a general sense), were shown in full lines, while all endoskeletal parts, such as phragmas, and all sutures covered over by other parts, such as appendages, were shown in the dot-and-dash line. In most figures the amount of development of the phragma between the meso- and the metatergum also was represented in this manner. Indistinct sutures and boundaries of chitinized areas which shade off into membrane, or vice versa, were represented by dotted lines. Spiracular openings were shown either with a crosshatched interior or with a fringed border.

Pencil drawings were inked on the coordinate paper and plates were made directly from these. Drawings were either enlarged or reduced in order that all plates might have one dimension, the length, uniform. Prints were made on contrast paper and the sclerites were labeled on these reproductions.

MATERIAL

The material on which this paper is based was all drawn from the collections in the Department of Entomology at Cornell University. Dissections have been preserved in alcohol and retained for reference.

For the convenience of systematists the figures are arranged in the order of the families to which each species belongs, as listed in Aldrich's *Catalogue of North American Diptera*.

Of the fifty-nine families according to Aldrich, one or more species from fifty-five have been studied and figured. In addition *Sciara ochrolabis* and *Psychoda cases*, which are included by Aldrich under the families Mycetophilidae and Sepsidae, respectively, are figured and placed in the families Sciaridae and Psychodidae. The following families are not represented. Acanthomeridae, Apioceridae, Phycodromidae, and Nycteri-

biidae. The list which follows gives the family, the species, the sex, and a reference to the drawings made of each. In addition, information gathered during the study as to the number of abdominal spiracles and their location in membrane or chitin is included.

Order *Diptera*

Division *Proboscidae*

Orthorrhapha — Nemocera

Tipulidae. *Pedicia albivitta*, female (Plate IX, 1 and 2), eight abdominal spiracles, all but last in membrane. It is possible that the supposed eighth spiracle may be the central attachment of the tracheal system to the tergite.

Pachyrrhina ferruginea, male (Plate IX, 3), seven abdominal spiracles, all in membrane.

Rhyphidae. *Taleera bimaculis*, female (Plate X, 4), seven abdominal spiracles, all in membrane.

Dixidae. *Dixa modesta*, female (Plate X, 5), seven abdominal spiracles, all in membrane.

Psychodidae. *Psychoda sexnotata*, female (Plate X, 6), seven abdominal spiracles, all in membrane.

Chironomidae. *Chironomus fenestratitta*, male (Plate XI, 7 and 8), at least seven and possibly eight abdominal spiracles, all in membrane.

Culicidae. *Culex canadensis*, male (Plate XI, 9), seven abdominal spiracles, all in membrane.

Anopheles quadrimaculata, female (Plate XII, 10), seven abdominal spiracles, all in membrane.

Corethra albipes, female (Plate XII, 11), seven abdominal spiracles, all in membrane.

Mycetophilidae. *Leia scutellata*, female (Plate XII, 12), seven abdominal spiracles, all in membrane.

Sciaridae. *Sciara ochreiventris*, male (Plate XIII, 13), seven abdominal spiracles, all in membrane.

Cecidomyiidae. *Rhabdophaga strobiloides*, male (Plate XIII, 14), seven abdominal spiracles, all in membrane.

Bibionidae. *Plecia heteroptera*, female (Plate XIII, 15), eight abdominal spiracles, seven in membrane.

Simuliidae. *Simulium hirtipes*, male (Plate XIV, 16), seven abdominal spiracles, all but first in membrane.

Blepharoceridae. *Blepharocera texana*, female (Plate XIV, 17), seven abdominal spiracles, all in membrane.

Orphnephilidae. *Orphnephila americana*, female (Plate XIV, 18), seven abdominal spiracles, all in membrane. Semblance of eighth spiracle indicated by color but no spiracular opening to be seen.

Orthorrhapha — Brachycera

Stratiomyiidae. *Allognota fusciarsis*, female (Plate XV, 19), seven abdominal spiracles, all in membrane.

Tabanidae. *Chrysops indus*, male (Plate XV, 20), seven abdominal spiracles, all in membrane.

Leptidae. *Chrysopila ornata*, male (Plate XV, 21), seven abdominal spiracles, all in membrane.

Nemestrinidae. *Hirmoneura* sp., female (Plate XVI, 22), seven abdominal spiracles, all in membrane.

Cyrtidae. *Oncodes incultus*, female (Plate XVI, 23), six abdominal spiracles, all in chitin

Bombyliidae. *Anthrax alternata*, female (Plate XVI, 24), seven abdominal spiracles, all in membrane.

Therevidae. *Thereva fucata*, male (Plate XVII, 25), seven abdominal spiracles, all in membrane.

Scenopinidae. *Scenopinus fenestralis*, female (Plate XVII, 26), at least seven and possibly eight abdominal spiracles, probably all in membrane, although those of last four segments (considering eight spiracles) are very close to the chitinous margin of the sternites.

Mydaidae. *Midas clavatus*, female (Plate XVII, 27), eight abdominal spiracles, all in membrane except last which is surrounded by chitin.

Asilidae. *Leptogaster lucri*, female (Plate XVIII, 28), at least seven and possibly an eighth abdominal spiracle, all except eighth in membrane

Dolichopodidae. *Didachopus cupreus*, male (Plate XVIII, 29), seven abdominal spiracles, all in membrane.

Empididae. *Rhamphomyia* sp., female (Plate XVIII, 30), seven abdominal spiracles, all in membrane

Lonchopteridae. *Lonchoptera* sp., female (Plate XIX, 31), seven abdominal spiracles, last four in membrane.

Phoridae. *Phora concinna*, female (Plate XIX, 32), at least six and possibly seven abdominal spiracles, all in membrane.

Cyclorrhapha — Athericera

Platypezidae. *Platypeza rebutina*, female (Plate XIX, 33), seven abdominal spiracles, first, fifth, sixth, and seventh in membrane.

Pipunculidae. *Pipunculus atlanticus*, female (Plate XX, 34), seven abdominal spiracles, all in membrane.

Syrphidae. *Sirphus americanus*, male (Plate XX, 35), seven abdominal spiracles, all in membrane.

Conopidae. *Myopa vesiculosa*, male (Plate XX, 36), seven abdominal spiracles, all but sixth and seventh in membrane.

Cyclorrhapha — Calyptratae

Oestridae. *Gastrophilus intestinalis*, female (Plate XXI, 37), seven abdominal spiracles, all in membrane

Tachinidae. *Tachina mella*, female (Plate XXI, 38), seven abdominal spiracles, sixth only in membrane although first is in very light chitin.

Dexiidae. *Thelaira nigripes*, male (Plate XXI, 39), seven abdominal spiracles, probably all in chitin although first, sixth, and seventh are in very light chitin.

Sarcophagidae. *Sarcophaga communis*, male (Plate XXII, 40), seven abdominal spiracles, first and sixth alone in membrane.

Muscidae. *Muscina stabulans*, female (Plate XXII, 41), seven abdominal spiracles, first, sixth, and seventh only in membrane.

Anthomyidae. *Macrorchis ausoba*, male (Plate XXII, 42), seven abdominal spiracles, all in chitin.

Chortophila cilicrura, male (Plate XXIII, 43), seven abdominal spiracles, first and sixth in membrane.

Hylephila pluvialis, female (Plate XXIII, 44), seven abdominal spiracles, first, sixth, and seventh in membrane.

Schoenomyza dorsalis, female (Plate XXIII, 45), apparently only five abdominal spiracles, all in chitin. Small species, caudal spiracles may have been overlooked.

Ophyra leucostoma, male (Plate XXIII, 46), seven abdominal spiracles, first and sixth only in membrane.

Lispa scalaris, female (Plate XXIII, 47), but five abdominal spiracles, first only in membrane.

Limnophora septentrionis, male (Plate XXIII, 48), seven abdominal spiracles, sixth only in membrane.

Eremoneura pyste (?), female (Plate XXIV, 49), seven abdominal spiracles, first only in membrane, although last two, which are rather close together, penetrate very little chitin.

Pegomyia affinis, female (Plate XXIV, 50), seven abdominal spiracles, first only in membrane, although last two, which are close together, penetrate very little chitin.

Hylemyia brevis, female (Plate XXIV, 51), seven abdominal spiracles, first only in membrane, although sixth and seventh are located very close together in the weak chitin of the first telescoped segment of the ovipositor.

Anthomyia calcium, male (Plate XXIV, 52), seven abdominal spiracles, first and sixth in membrane.

Hebecnema subalpina, female (Plate XXIV, 53), but five abdominal spiracles found, first only in membrane.

Fannia canicularis, male and female, seven abdominal spiracles, first only in membrane.

Cyclorrhapha — Acalyptratae.

Scatophagidae. *Scatophaga furcata*, male (Plate XXV, 54), seven abdominal spiracles, first and seventh in membrane.

Heteroneuridae. *Chiura lateralis*, female (Plate XXV, 55), seven abdominal spiracles, first two in membrane.

Helomyzidae. *Leria serrata*, male (Plate XXV, 56), seven abdominal spiracles, all in membrane.

Borboridae. *Borborus equinus*, female (Plate XXVI, 57), seven abdominal spiracles, all in membrane.

Sciomyzidae. *Dictya umbrarum*, female (Plate XXVI, 58), seven abdominal spiracles, all but last two in membrane.

Sapromyzidae. *Sapromyza lupulina*, male (Plate XXVI, 59), seven abdominal spiracles, all in membrane.

Ortalidae. *Rivellia viridulans*, female (Plate XXVII, 60), seven abdominal spiracles, all but last in membrane.

Rhopalomeridae. *Rhopalomera flaviceps*, female (Plate XXVII, 61), seven abdominal spiracles, all in membrane.

Trypetidae. *Euaresta festiva*, female (Plate XXVII, 62), seven abdominal spiracles, all but last in membrane.

Micropezidae. *Calobata albiceps*, female (Plate XXVIII, 63), seven abdominal spiracles, all but last in membrane.

Sepsidae. *Sepsis rufacea*, female (Plate XXVIII, 64), seven abdominal spiracles, all but last two in membrane.

Piophilidae. *Prochila casei*, female (Plate XXVIII, 65), seven abdominal spiracles, all in membrane.

Psilidae. *Loxocera pleuritica*, male (Plate XXIX, 66), seven abdominal spiracles, all in membrane.

Diopsidae. *Sphyrocephala brevicornis*, female (Plate XXIX, 67), seven abdominal spiracles, all in membrane.

Ephydridae. *Perygra limpidipennis*, female (Plate XXIX, 68), six abdominal spiracles, first only in membrane.

Oscinidae. *Chlorops* sp., male (Plate XXX, 69), six abdominal spiracles, first, second, and sixth only in membrane.

Drosophilidae. *Drosophila melanogaster* (?), female (Plate XXX, 70), seven abdominal spiracles, all in membrane.

Geomyzidae. *Anthomyza gracilis*, female (Plate XXX, 71), six abdominal spiracles found, all in membrane. Specimen so small that it was hard to be sure of no seventh spiracle.

Agromyzidae. *Agromyza lateralis*, male (Plate XXXI, 72), seven abdominal spiracles, all but last two in membrane. In female of species all but last one of seven spiracles are in membrane.

Division *Eproboscidae*

Hippoboscidae. *Melophagus ovinus*, female (Plate XXXI, 73), seven abdominal spiracles, all in membrane.

Olfersia americana, female (Plates XXXI, 74, and XXXII, 75), seven abdominal spiracles, all in membrane.

Order *Mecoptera*

Panorpidae. *Panorpa venosa*, female (Plate XXXII, 76), eight abdominal spiracles all in membrane.

TERMINOLOGY

The rule of priority in the selection of anatomical terms is recognized in this paper only to the extent that these are descriptive of the parts to which they refer, or else have been so generally accepted by workers

in the group that the use of another more descriptive term would add to the confusion already existing in the nomenclatures of different orders of insects.

Full lines representing sutures in drawings are not limited to any one kind of suture, but to sutures in general, whether these are spaces between approximated sclerites or plates of the integument, impressed lines, or lines formed by the approximated lips of an infolding of the body wall.

GENERALIZATIONS

The scope of this investigation makes it necessary to limit the discussion of homologies to the metathorax and the first few abdominal segments; consequently many interesting modifications and details of structure in the remaining thoracic segments which have been figured may prove of advantage to those interested in the order, but must be disregarded at present by the writer. However, sclerites have been named in the mesothorax according to the dictates of this study, and a short discussion of the terms employed will of necessity be given.

If the Apterygote are to be considered the most generalized insects forms in which wings were never present and therefore forms in which the muscular tension and mechanical stimulus due to the proper functioning of these locomotor appendages has never been experienced and a thoracic segment of such an insect in which there is practically no chitin laid down in the membrane is to be considered as rather primitive then our conclusion must be that a membranous condition must have been that of the thoracic segments of primitive insects, and only when the development of appendages gave rise to muscular stresses and strains and friction of parts was it necessary that their walls should be strengthened by the deposition of chitin in their integument. All theories to the origin of insects from annelid-like ancestors tend to strengthen this hypothesis. *Panorpa venosa* (Plate XXXII, 76), therefore, has been figured simply to show the appearance of a more primitive winged form. The development of wings has meant the chitinization of terga and pleura, together with the invagination of the body wall to form the pleural ridges, while the increase in size of the legs has meant their chitinization and their division into the true coxae and mera. The straightness of the pleural and coxal ridges is a mark of primitiveness. The large amount of membrane in the abdomen is another, while the distinctiveness of the basalares and the subalares might be considered a third. The two divisions of each tergum of the

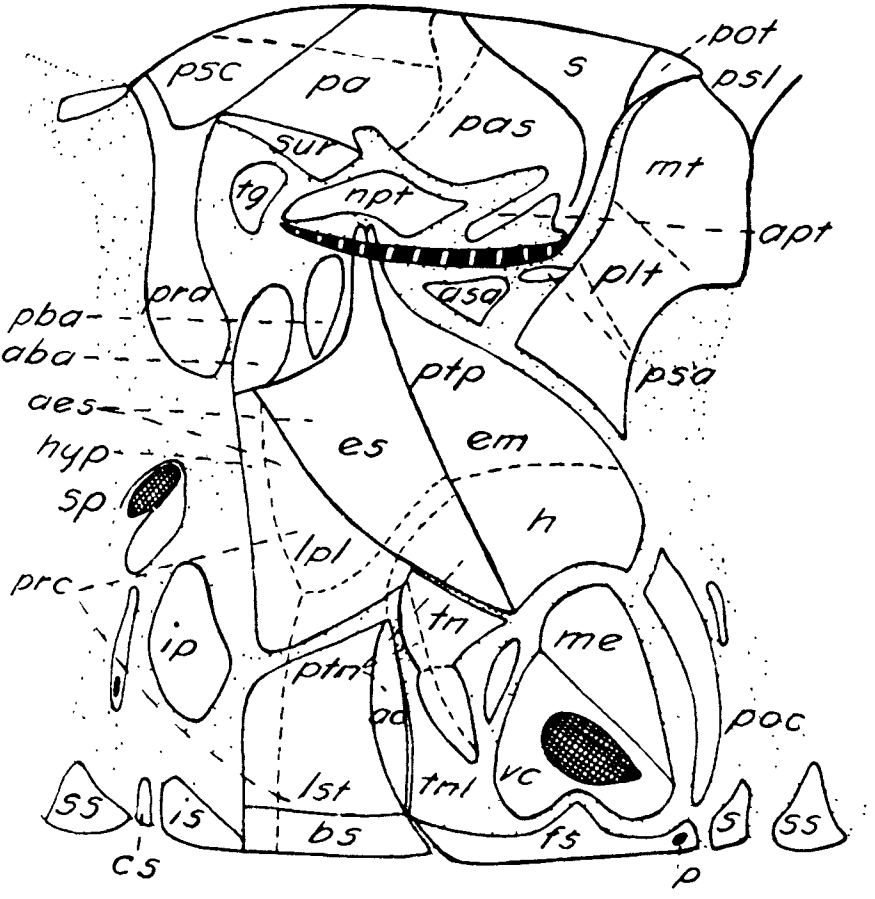

FIG. 21. GROUND PLAN OF A TYPICAL THORACIC SEGMENT IN WINGED INSECTS
(After Crampton, 1914,b)

meso- and the metathorax are clearly set off from each other, while the beginning in the development of phragmas is seen in both the anterior and the posterior infolding of the walls of the terga of these two thoracic segments. The maximum development of phragmas can be seen in the posterior mesothoracic and the anterior metathoracic one in some dipterous species.

For convenience in comparing, a copy of Crampton's (1914 b) "ground plan of a typical thoracic segment in winged insects" is here inserted (fig. 21). In the author's own words, this figure

> represents an hypothetical composite type, to which the thoracic segments of any insect can be referred as a basis of comparison, rather than an attempted reconstruction of the original condition of the thoracic sclerites in the ancestors of winged insects. Most of the primitive features, however, are included in the figure, and to these have been added conditions found in the more specialized insects.

DISCUSSION OF PARTS

The mesothorax

The tergum

The two plates of the tergum as described by Verhoeff (1902) and by Snodgrass (1909 a) are readily distinguished in all forms figured. The large anterior plate, extending backward and including the axillary cord of Snodgrass (1909 b) and the post-tergite of Crampton (1914 b), composed largely of the scutum and the scutellum, has been called the scuto-scutellum when there are no visible divisions. Audouin (1824) has been followed herein in his divisions of the scuto-scutellum. The most anterior median region is termed the prescutum. The large central region, which is very often fused with the prescutum and also often subdivided by secondary sutures, is called the scutum. Laterally this division carries both the anterior and the posterior notal wing processes of Snodgrass, both of which are usually well defined in Diptera. The third division, known the scutellum, is fairly constant as a narrow elevated median plate extending laterally into a narrow band bearing the axillary cord, which is continuous with the anal margin of the wing.

The small caudal division of the tergum when not divided is termed the postscutellum. This plate is often divided by sutures into a median and one or two lateral sclerites. When such is the case, only the abbreviations for these divisions appear on the drawings. For the middle plate the term *mediotergite* (mtg.) and for the lateral plate or plates the term *pleu-*

tergite (plt), are used. These are the terms which Crampton appropriates from Martin. In case there are two lateral plates formed, the writer has prefixed *ana* and *kata* to the term *pleurotergite* for the upper and lower subdivisions, respectively, calling the upper one *anapleurotergite* (aplt) and the lower one *katapleurotergite* (kplt).

The anterior phragma (Plate XXXII, 76, phg^2_a), or internal fold of the terga between the pro- and the mesothorax, is usually poorly developed in this group, and for this reason it is not indicated in the drawings. When present it usually projects under the pronotum. The posterior phragma (Plate XXXII, 76, phg^2_p) is well developed in the Brachycera (Plates XV, 21, and XVI, 21). Very frequently the two lamellae, the one of the mesonotum and the other of the metanotum, are easily distinguishable in the composition of this phragma.

The pleuron

Primarily the pleuron plate is composed of two sclerites, the episternum (es^2) and the epimeron (em^2). The suture (pleural) formed by a more or less transverse infolding of the walls of this plate (Plates IX, 1, and XI, 8, ap^2) divides it into an anterior part, the episternum, and a posterior region, the epimeron. This suture in its primitive condition extends from the wing process to the coxa, but in some of the higher Diptera, as *Musca stabulans* (Plate XXII, 11), it may disappear altogether just above the leg. The primitive straightness of this suture as shown in *Panorpa venosa* (Plate XXXII, 75), in the Tipulidae (Plate IX, 3), in the Rhyphidae (Plate X, 4), in the Culicidae (Plate XII, 10), and in other forms, gives way in the more specialized members of the group to a prominent forward bending, in some cases, about midway dorsad from its origin at the coxa (Plates XX, 35, and XXII, 42).

Secondary sutures may divide either the episternum or the epimeron, or both, into a dorsal and a ventral region, and in some cases the dorsal episternal area into an anterior and a posterior part. If common usage did not dictate differently, the writer would prefer to use the more descriptive prefixes *ana* and *kata* combined with the names of the primary sclerites in referring to these secondary divisions, and simply refer to the secondary division of the dorsal episternum as the *anterior anepisternum*. But because of their widespread acceptance by systematists of this group, the use of Osten-Sacken's (1884) terms *pteropleura* and *sternopleura* —

slightly modified to *pteropleurite* (ptp^2) and *sternopleurite* (stp^2) as suggested by Crampton (1914 b) for *anepimeron* and *katepisternum*, respectively — seems advisable. Furthermore, Crampton's term *hypoepimeron* (hem^2) has been accepted on the same grounds. This leaves only the anepisternum to retain the more descriptive name, its anterior part being labeled "aes_a^2" and its posterior part when present being referred to as "aes_p^2."

The generalized type of coxa as illustrated in *Panorpa venosa* (Plate XXXII, 76) — in which the pleural suture is continuous throughout the length of this first segment of the leg, dividing it into the true coxa (cx^2) and the meron (me^2), terms used by Walton (1900) — is to be recognized only in a few of the lowest families of flies, as the Tipulidae (Plate IX, 2 and 3) and the Rhyphidae (Plate X, 4). In the last two figures evidence is given of the migration of the meron dorsad to become fused eventually with the lower pleural sclerite, the hypoepimeron. In all the higher families of flies this interpretation is placed on the fate of the meron, and the combined meron and hypoepimeron is termed, after Crampton (1914 b), the *mesopleurite* (mep^2).

The basalare and subalare sclerites are often present in this order and are figured herein, although not labeled in most of the drawings.

The sternum

To the writer's mind it seems doubtful whether the term *sternopleurite* should be used as its author intended, that is, to refer to a combined sternal and pleural sclerite, or rather to the part of the pleurite which borders on the sternum. The study of the venter of flies is carried on with difficulty because of the proximity of the bases of the legs. But a number of the broader representatives of the group show the same arrangement of sclerites as does *Olfersia americana* (Plate XXXII, 75), in which the two pleurites termed *sternopleurites* meet each other on the ventral side, apparently crowding out the anterior part of the sternum — the *basisternite* (bs of Crampton (1909)). The furcasternite (fs) alone seems to remain in this group.

The metathorax

The tergum

Compared with those of the mesothorax, all three plates of the metathorax are very small. As has been suggested, the large development of

the mesothorax to take care of the powerful wing muscles seems to have taken place at the expense of the following thoracic segment. Especially is this evident in the tergal region, which usually consists of a narrow band of integument connecting the two halteres and providing a single lamella cephalad as its share in the formation of the mesothoracic postscutellar phragma (phg^2_p). It is impossible to make out the four principal subdivisions of the tergum in the metathorax of Diptera. This plate reaches its greatest development in *Psychoda slossoni* (Plate X, 6), so far as the writer's studies have gone. It may be continuous with the epimeron of this segment, as in *Plecia heteroptera* (Plate XIII, 15), *Scenopinus fenestralis* (Plate XVII, 26), *Leptogaster loewi* (Plate XVIII, 28), and many other species, or there may be a suture separating these two sclerites, as in *Anthrax alternata* (Plate XVI, 24), *Platypeza velutina* (Plate XIX, 33), *Macrorchis ausoba* (Plate XXII, 42), and many others; but practically in every case the tergum is separated from the episternum in this segment by the pleural suture.

The pleuron

Although comparatively small sclerites, the episternum (es^3) and the epimeron (em^3) are separated in the metathorax, as in the mesothorax, by the pleural suture. This infolding of the body wall is fairly constant in its extent from the coxae to the base of the halteres, and, studied from the inside, affords one of the best landmarks for homologizing these sclerites. Occasionally in the more generalized species the presence of secondary sutures in the episternal sclerite makes necessary the use of the terms *anepisternum* (aes^3) and *katepisternum* (kes^3), as in *Pachyrrhina ferruginea* (Plate IX, 3) and *Leia winthemi* (Plate XII, 12). Secondary sutures are present also in the posterior pleural sclerite, as in *Dixa modesta* (Plate X, 5) and *Culex canadensis* (Plate XI, 9), but because of the uncertainty as to the line of demarcation between the postscutellum and the epimeron the single term *epimeron* (em^3) is used here.

A large number of peculiarities or variations in the shape of the pleural sclerites are to be found in the various families of this order. Chief among these might be mentioned the following. Commonest of all, perhaps, is a greatly developed episternum with a resulting small epimeron, often nothing more than a narrow strip of chitin and in some cases resulting in the lower part of the epimeron becoming membranous throughout.

Examples of such a development are found in Plates IX, 2, X, 4, 5, and 6, XI, 7, XII, 12, XIII, 13, 14, and 15, XIV, 18, XVII, 27, and XIX, 32. On the other hand, there are examples of the opposite development, the epimeron becoming greatly enlarged at the expense of the episternum, as in *Dolichopus caprinus* (Plate XVIII, 29).

Another common peculiarity in the epimeral region is the failure of the hypodermal cells of the ventral part of this area to lay down chitin in the integument, with the resulting appearance of the epimeron's moving dorsad (Plates X, 6, XI, 7, XIII, 14, XIV, 16, 17, and 18, XIX, 32, XX, 34 and 35, XXVI, 57, XXVII, 62, XXIX, 67). Many examples of very weak chitin in this lower epimeral sclerite are to be seen. In fact, it is often difficult to say where the epimeron leaves off and the intersegmental abdominal membrane begins (Plates XIII, 13, XXI, 38 and 39, XXII, 41, XXX, 70 and 71, XXXI, 72).

An interesting variation in the lower Nemocera, and one that is very difficult of interpretation, is the movement cephalad of the episternum (es) into the mesothorax, with a resulting crowding of the compound sclerite mep into a very small area above the mesothoracic coxa (Plates X, 5 and 6, XI, 9, XII, 10 and 11).

The movement forward of both pairs of legs has caused a decided prolongation of both the episternum (es) and the epimeron (em^3) in *Leptogaster lowei* (Plate XVIII, 28) and in *Gastrophilus intestinalis* (Plate XXI, 37); while the prolongation of the coxae in *Leia winthemi* (Plate XII, 12) apparently results in the movement of the episternum (es^3) and the epimeron (em^3) down on the base of the legs.

Sutures sometimes become vestigial, as in the case of *Oncodes incisus* (Plate XVI, 23) in which the pleural suture shows no implex nor scale or any external evidence of having once existed just above the base of the coxa. The suture between the lower epimeron of the mesothorax and the metathoracic episternum is lacking in *Dixa modesta* (Plate X, 5) and in *Phora contorta* (Plate XIX, 32).

What seemed to be sense pits were found on a number of species on either the tergum or the pleuron of the metathorax or the basic segments of the abdomen. In a number of cases these have been figured, as in *Thereva fucata* (Plate XVII, 25, em^3 and 28), in *Leptogaster lowei* (Plate XVIII, 28, t^3), in *Chrysopila ornata* (Plate XV, 21, 2t), and in *Hermetia* sp. (Plate XVI, 22, 2t and 28).

The course of the metathoracic apodeme (Plate XI, 8, ap^3), together with the locations of the metathoracic spiracles (sp^3) and the first abdominal spiracle (1sp), has been a great aid in deciding on these relationships.

Besides the episternum and the epimeron, there is a third pleural sclerite in the metathorax of Diptera which seems to correspond to Crampton's (1914 b) compound sclerite, the pleurotrochantin (fig. 21, ptn.) This compound sclerite is described as being composed of the antecoxale (ac) — which is a narrow marginal strip of the basisternite — the trochantinelle (tnl), the trochantin (tn), and the lower part of the episternum. This sclerite is present in a large number of the higher Diptera, and especially is well marked in the acalyptrate muscids, as *Loria serrata* (Plate XXV, 56, ptn^3), *Rivellia viridulans* (Plate XXVII, 60, ptn^3), and *Sphyracephala brevicornis* (Plate XXIX, 67, ptn^3).

The sternum

As in the mesothorax, the furcasternite — the sternal region which bears the internal diapophyses, or furcae (Plate IX, 1, $apys^3$) — seems to be the only sternite remaining in the order. A glance at the ventral view of *Oltersia amarica* (Plate XXXII, 75) will show the marginal lips of the two sclerites termed *pleurotrochantin* (ptn^3) meeting in the mid-ventral line but separating caudad to form the furcasternite (fs^3).

The legs

In no case was the metathoracic coxa found divided by a suture into the true coxa and the meron. If muscular tension causes the ridges of the body wall to be drawn inward for the formation of phragmas, apodemes, and apophyses, this may give a partial explanation of the disappearance of a suture dividing the coxa into two subdivisions, as the metathoracic muscles are greatly reduced in size due to the replacement of the wings by the halteres.

Nothing further need be said concerning the metathoracic legs, except that the coxae show the greatest variation. *Lena wiedemi* (Plate XII, 12, cx^3) and *Sciara ochrolabis* (Plate XIII, 13, cx^3) show a considerably elongated condition. In *Blepharocera tenuipes* (Plate XIV, 17, cx^3) the coxae assume a diagonal position between the thorax and the trochanter, while innumerable variations in shape exist. A number of the Acalyptratae show this part of the leg fairly well sculptured with secondary external sutures,

as in *Scatophaga stercoraria* (Plate XXV, 54, cx³), *Dictya umbrarum* (Plate XXVI, 58, cx³), and *Sapromyza lupulina* (Plate XXVI, 59, cx³).

The abdomen

General description

In taking up the discussion of the morphology of the abdomen in its relation to the thorax, the tergites, the sternites, and the spiracles are considered separately. There is little to be said in regard to the pleura aside from the fact that they are commonly taken as the membranous areas between chitinized tergites and sternites. Needless to say, this region shows a considerable variation in width in species showing some deposition of chitin in the sternites and the tergites. A comparison of *Calobata albiceps* (Plate XXVIII, 63) with one of the calyptrate muscids, as *Thelaira nigripes* (Plate XXI, 39), will at once show a wide difference. In the latter example the pleura consist only of narrow inflexed areas between the greatly enlarged tergites and the small sternites which they have overgrown. In the case of species showing no deposition of chitin in the sternal region, as *Phora concinna* (Plate XIX, 32) and *Chlorops* sp. (Plate XXX, 69), and in species showing no deposition of chitin in either the tergal or the sternal region, as *Orphnephila americana* (Plate XIV, 18), *Melophagus ovinus* (Plate XXXI, 73), and *Ornithomyia americana* (Plate XXXI, 74), it is impossible to speak of a definitive pleuron.

In homologizing the sclerites in the abdomen of Diptera the position of the spiracles is of invaluable aid. In fact, it would be next to impossible to be sure of the sclerites of the first segment without the location of the first abdominal spiracle. An internal study is often necessary to establish the position of this opening to the tracheal system.

In this order, usually five more or less definite abdominal segments may be seen. Beyond the fifth the segments are variously modified to form the genitalia. For this reason it is very easy to overlook spiracles beyond the fifth, as these are often small and show a tendency toward cephalization. It is not unusual to find those of successive segments crowded close together in the same segment in this region.

The tergites

There are many interesting features in the structure of the abdominal tergites. In looking at the group as a whole, it is quite evident that there is a tendency for the first tergite, as well as for the first ster-

to decrease in relative size. This one is usually nothing more than a narrow band as compared with those that follow. (Plates IX, 2 and 3, X, 1, XIV, 17, XVI, 22, XVII, 26, XVIII, 28 and 30, XX, 35.) Nor can all of this decrease be attributed to the failure of the hypodermal cells to deposit chitin in the membrane just cephalad of the first tergite. It seems very probable that the belief that one segment may gradually disappear owing to the great development of a contiguous segment, is sometimes warranted.

This theory of growth of one segment at the expense of an adjoining one might at first seem to be very good evidence for use in determining what has happened in case of species which show but one chitinized tergite to two spiracles, such as *Lonchoptera* sp. (Plate XIX, 31, 1t and 2t), *Macrorchis ausoba* (Plate XXII, 42, 1t and 2t), *Euaresta festiva* (Plate XXVII, 62, 1t and 2t), *Calobata albiceps* (Plate XXVIII, 63, 1t and 2t), *Sepsis violacea* (Plate XXVIII, 64, 1t and 2t), *Piophila casei* (Plate XXVIII, 65, 1t and 2t), and *Sphyracephala brevicornis* (Plate XXIX, 67, 1t and 2t). But on considering the large number of examples that might be regarded as transitional stages between the well-defined first and second tergite, on the one hand, and the single tergite to represent both, on the other hand, it is easier to believe in a fused condition of these two tergites than in the alternative which would permit the second, or larger, tergite to crowd out the first, or smaller, one altogether. These transitory stages may be seen in a number of species. In *Platypeza velutina* (Plate XIX, 33) there appear two notches in the latero-ventral margin of the tergites at about the place where one would expect to find a dividing suture, and only a lighter band can be seen extending up through the middle of the tergites. In *Pipunculus atlanticus* (Plate XX, 34) the only remaining sign of a suture is a very faint impressed line. In *Tachina mella* (Plate XXI, 38), only a lighter-colored band marks what may have been the position of a suture in its progenitors. This is likewise the case in *Sarcophaga communis* (Plate XXII, 40). Very faint impressed lines exist in *Thelaira nigripes* (Plate XXI, 39), in *Muscina stabulans* (Plate XXII, 41), and in *Dictya umbrarum* (Plate XXVI, 58). Latero-ventral incisions, sometimes with and sometimes without vestigial sutures, are to be seen in some species, as *Sapromyza lapulina* (Plate XXVI, 59), *Parydra limpidipennis* (Plate XXIX, 68), *Chlorops* sp. (Plate XXX, 69), and *Drosophila melanogaster* ♂ (Plate XXX, 70). A vestigial suture exists in *Rivellia viridulans* (Plate XXVII, 60), while only a bit of membrane is to be found in such

species as *Borborus equinus* (Plate XXVI, 57), *Rhopalomera flavipes* (Plate XXVII, 61), and *Loxocera pleuritica* (Plate XXIX, 66). These and other examples that might be cited seem to warrant the consideration of this first definitive tergite as the fused first and second tergites. In unbleached specimens these indications of a suture would hardly be noticed, and so it is not to be wondered at that systematists of the order do not always agree as to the number of abdominal segments.

Another possible source of confusion to the systematist is to be found in the division of tergites into secondary parts, either by sutures or a strip of membrane. This may occur in either the first or the second segment. As an example of a tergite being divided into two subdivisions by a suture, one need only refer to the drawings of *Simulium hirtipes* (Plate XIV, 16, $1t_a$ and $1t_p$) and *Midas clavatus* (Plate XVII, 27, $1t_a$ and $1t_p$). Examples of division by membrane may be seen in *Sciara ochrolabis* (Plate XIII, 13, $1t_a$ and $1t_p$) and in *Phora heteroptera* (Plate XIII, 15, $2t_a$ and $2t_p$). An example of the separation of the first and second tergites by a narrow band of membrane or weak chitin is given in *Allognosta fuscitarsis* (Plate XV, 19).

In several species the first abdominal tergite has so overgrown the thorax that on superficial examination it appears as a part of this region. This condition is most evident in such species as *Chrysops indus* (Plate XV, 20, 1t) and *Anthrax albicosta* (Plate XVI, 24, 1t).

A very noticeable character, and one that was first found in *Myopa vesiculosa* (Plate XX, 36), is an adventitious suture arising from the latero-cephalic margin of the first abdominal tergite and running caudo-dorsad through this tergite often to the cephalic margin of the second tergite. This varies considerably in its degree of development in different species, but was found in all the species examined among both the Calyptratae and the Acalyptratae. Generally speaking, this suture is less highly developed in the calyptrate than in the acalyptrate muscids, as is seen on comparing *Thelaira nigripes* (Plate XXI, 39) and *Musca stabulans* (Plate XXII, 41) with *Scatophaga stercoraria* (Plate XXV, 54) and *Sepsis violacea* (Plate XXVIII, 64).

The sternites

The greater demand made upon the tergites for the attachment of muscles than upon the sternites is clearly reflected in the larger num-

of species found in which the sternites were composed of membrane or very weak chitin. In so far as the tergites are concerned, these are of such a composition only in *Orphnephila americana* (Plate XIV, 18); while the following species show this condition in so far as the sternites are concerned: *Simulium hirtipes* (Plate XIV, 16), *Orphnephila americana* (Plate XIV, 18), *Phora concinna* (Plate XIX, 32), *Gastrophilus intestinalis* (Plate XXI, 37), *Chlorops* sp. (Plate XXX, 69), *Melophagus ovinus* (Plate XXXI, 73), and *Olfersia americana* Plate XXXI, 74). Instances of the first abdominal tergite remaining membranous, possibly to facilitate the movement of the caudal end of the abdomen, are not uncommon. This is the case in *Anopheles quadrimaculata* (Plate XII, 10), *Midas clavatus* (Plate XVII, 27), *Lonchoptera* sp. (Plate XIX, 31), *Pipunculus atlanticus* (Plate XX, 34), and *Borborus equinus* (Plate XXVI, 57). Other species, such as *Rhabdophaga strobiloides* (Plate XIII, 14) and *Drosophila melanogaster* (?) (Plate XXX, 70), have a slight amount of chitin laid down in this sternite.

The same forces that have had their effect in decreasing the size of the first abdominal tergites have produced the same result in the sternites of a larger number of species. Most decidedly is this the case in *Trichocera hiemalis* (Plate X, 4, 1s), in *Thereva fucata* (Plate XVII, 25, 1s), in *Scenopinus fenestralis* (Plate XVII, 26, 1s), in *Leptogaster locwi* (Plate XVIII, 28, 1s), in *Dolichopus cupreus* (Plate XVIII, 29, 1s), and in *Muscina stabulans* (Plate XXII, 41, 1s); while the same condition holds to a lesser extent in *Leia winthemi* (Plate XII, 12, 1s), in *Sciara ochrolabis* (Plate XIII, 13, 1s), in *Hæmoxena* sp. (Plate XVI, 22, 1s), and in *Sarcophaga communis* (Plate XXII, 40, 1s).

Subdivisions of primary sternites are found oftener than are subdivisions of primary tergites, the second sternite being the one oftenest modified in this way. In *Pachyrhina ferruginea* (Plate IX, 3, $1s_a$ and $1s_p$), in *Phora heteroptera* (Plate XIII, 15, $2s_a$ and $2s_p$), in *Rhamphomyia* sp. (Plate XVIII, 30, $2s_a$ and $2s_p$), and in *Calobata albiceps* (Plate XXVIII, 63, $2s_a$ and $2s_p$), the anterior part is separated from the posterior part of the second sternite by membrane.

In only one species, *Chrysops indus* (Plate XV, 20, 1s and 2s), were the first and second sternites found to have coalesced. Here a double row of sense pits marks the usual position of the suture between the first and the second segment.

The spiracles

The number of abdominal spiracles in Diptera varies from five to eight, with seven as the number oftenest met with. Data on this point are given in the list of species on pages 258 to 261. A glance at these data will show these openings to the tracheal system appearing either in membrane or in chitin, but oftener in membrane, as would be expected when it is considered that the normal position of the row of abdominal spiracles may be assumed to be midway between dorsum and venter in the latus. In a large majority of families this region remains membranous, and only in relatively few have the so-called tergites usurped the pleural region enough to include the spiracles. It amounts to this: when the hypodermal cells in the pleural region have become stimulated enough to deposit chitin, then, in the order Diptera, this region forfeits its right to be known as a part of the pleuron and must be called a part of the tergum. This arrangement of spiracles in the order certainly goes to show that if for any reason there is need for rigidity in a certain region, it is no more difficult to lay down chitin around spiracles than at any other place.

As a rule it may be said that the abdominal spiracles of species of the Nemocera and Brachycera groups in the suborder Orthorrhapha are to be found in membrane. But immediately the outstanding exceptions, in so far as the writer's study has gone, would have to be mentioned in *Oncodes incultus* (Plate XVI, 23) and in *Lonchoptera* sp. (Plate XIX, 31). In the suborder Cyclorrhapha, the representative families of the Athericera and the Acalyptratae tend to permit their abdominal spiracles to remain in membrane. A number of exceptions would have to be raised here, however, such as *Platypeza volutina* (Plate XIX, 33), *Pseudobaptisbaptidoptenis* (Plate XXIX, 68), and others. Among the families of the Calyptratae of this suborder, the tendency is toward the deposition of chitin about these spiracular openings because of the excessive downward extension of the tergites. It is needless to say that this is not the case in all species of every family in the group. A glance at the record of the species of anthomyids studied will expel any doubts concerning this last statement.

In most of the Diptera, and especially in the more generalized species, the first abdominal spiracle is to be found in the anterior part of the segment and very often in the membrane between the metathorax and the first abdominal segment. The usual position of the remaining spiracles is

near the middle of the segment, if anything slightly cephalad from the center. Such an arrangement as that in *Oncodes incultus* (Plate XVI, 23), in which the first abdominal spiracle appears in the posterior part of the segment, is very unusual, while examples of the shifting of all spiracles to the anterior end, as in *Allognosta fuscitarsis* (Plate XV, 19), is not at all uncommon.

SPECIES OF ANTHOMYIDS

Because of the uncertain systematic position of some genera within the family Anthomyiidae, species of twelve genera of this family were studied and figured (Plates XXII, 42, XXIII, and XXIV, inclusive). Considerable uniformity is shown in the structure of the region around the base of the abdomen. In each case were the episternum (es^3) and the epimeron (em^3), as well as the pleurotrochantin (ptn^3), of the metathorax clearly defined. The fused condition of the first and second abdominal tergites, in contrast to the separate state of the corresponding sternites, held in each. Also, the adventitious suture of the first abdominal tergite was constant. The greatest variation found in these species, perhaps, was in the location of the abdominal spiracles. This can be seen by referring to the information concerning abdominal spiracles which accompanies each species in the list on pages 258 to 261.

SUMMARY[2]

Points brought out in a summary of an investigation of this nature must of necessity be based upon a study of a rather limited amount of material, considering the number of genera and species in the entire order. However, uniformities existing in single species of so wide a range of families as the writer has been permitted to examine, will at least suggest points to be tested in a wider range of species within certain families. Furthermore, they cannot help adding their bit in the task of unraveling the phylogeny of the order Diptera.

One of the most interesting characteristics to appear in a large number of families is what has been termed an adventitious suture, or a suture running caudo-dorsad from the anterior margin of the first abdominal tergite and one not to be confused with the suture dividing the first and the second tergite although the two are closely related to each other.

[2] The chart from which this summary was deducted is inserted at the end of this paper.

This suture was found in species of all the families studied among the Calyptratae and the Acalyptratae, but in only one family outside of these two groups, in *Myopa vesiculosa* (Plate XX, 36) of the family Conopidae.

Closely associated with the appearance of this suture is a tendency toward the coalescence of the first two abdominal tergites. This tendency toward fusion occurs in all the families of the Acalyptratae with the exception of the Scatophagidae (Plate XXV, 54), the Heteroneuridae (Plate XXV, 55), and the Helomyzidae (Plate XXV, 56); and in all the families of the Calyptratae with the exception of the Oestridae (Plate XXI, 37). Aside from the families of these two groups it occurs only in the Conopidae (Plate XX, 36), the Pipunculidae (Plate XX, 34), the Platypezidae (Plate XIX, 33), and the Lonchopteridae (Plate XIX, 31). But at least five different stages in the development of this tendency can be pointed out if there are included the families showing both the adventitious suture and a complete suture between the first and second tergites, as the Oestridae (Plate XXI, 37), the Scatophagidae (Plate XXV, 54), the Heteroneuridae (Plate XXV, 55), and the Helomyzidae (Plate XXV, 56). The adventitious suture and only the dorsal part of the suture dividing the two tergites are found in the Conopidae (Plate XX, 36), the Sarcophagidae (Plate XXII, 40), the Sciomyzidae (Plate XXVI, 58), the Piophilidae (Plate XXVIII, 67), and the Geomyzidae (Plate XXX, 71). Further, the adventitious suture and only the ventral part of the suture dividing the first and second tergites are found in the Borboridae (Plate XXVI, 57), the Sapromyzidae (Plate XXVI, 59), the Ortalidae (Plate XXVII, 60), the Sepsidae (Plate XXVIII, 64), the Ephydridae (Plate XXIX, 68), the Oscinidae (Plate XXX, 69), and the Drosophilidae (Plate XXX, 70). The next stage would be represented by families showing the adventitious suture alone, in a few cases the suture between the tergites being represented by a semblance of membrane, as in the Tachinidae (Plate XXI, 38), the Dexiidae (Plate XXI, 39), the Muscidae (Plate XXII, 41), the Anthomyidae (Plate XXII, 42), the Rhopalomeridae (Plate XXVII, 61), the Trypetidae (Plate XXVII, 62), the Micropezidae (Plate XXVIII, 63), the Psilidae (Plate XXIX, 66), the Diopsidae (Plate XXIX, 67), and the Agromyzidae (Plate XXXI, 72). Finally, in some families no marked evidence of either suture was to be found, as in the Lonchopteridae (Plate XIX, 31), the Platypezidae (Plate XIX, 33), and the Pipunculidae (Plate XX, 34). Among the species of anthomyids

studied, two of these stages were represented, eight species showing the adventitious suture and the ventral part of the suture separating the first and second tergites, and four species showing only the adventitious suture.

In drawing conclusions regarding any uniformities existing among Diptera in respect to the location of abdominal spiracles, perhaps it would be best to disregard the first and those beyond the fifth segment, and consider only the second, third, fourth, and fifth segments. The integument in which the first abdominal spiracle is located is the most subject to change, as it is just at the point of attachment of the abdomen to the thorax. As there is a necessity for flexibility at this point, the body wall is usually membranous, and as a result the first abdominal spiracle is, with few exceptions, as in the cyrtid (Plate XVI, 23), the lonchopterid (Plate XIX, 31), the tachinid (Plate XXI, 38), the dexiid (Plate XXI, 39), and three species of anthomyids (Plates XXII, 42, and XXIII, 47 and 48), found in membrane. Beyond the fifth segment, the spiracles are so affected by the forces producing the modification of the segments into the genitalia that these too are unreliable. But in considering the second, third, fourth, and fifth spiracles in regard to location in membrane or chitin, some uniformities are seen. All four of these spiracles in each family of the Calyptratae except the Oestridae, in which they are in the membrane, are found in chitin. Among the Acalyptratae, all four spiracles in the Scatophagidae and the Ephydridae, and the third, fourth, and fifth in the Oscinidae, are found in chitin. All other represented families have these spiracles in membrane. Aside from these two exceptions, only scattered cases are found in which these spiracles are replaced by chitin. In the Cyrtidae, all four are in chitin; in the Lonchopteridae and the Platypezidae, only the third, fourth, and fifth are in chitin.

The pleuro-trochantin (ptn^{1}) of the metathorax appears as a chitinized sclerite in all the Cyclorrhapha, with the possible exception of the Oestridae (Plate XXI, 37), the Tachinidae (Plate XXI, 38), and the Pipunculidae (Plate XX, 34). Among the Brachycera there seem to be two families showing true chitin in this sclerite, the Asilidae (Plate XVIII, 28) and the Lonchopteridae (Plate XIX, 31). This sclerite appears as membrane or as questionable chitin, if at all, in all other families.

In a few families it was rather difficult to separate the epimeron of the metathorax from the sclerites of the first abdominal segment. These

species sometimes give one the impression that the epimeron of the metathorax is an abdominal sclerite and the first tergite is a thoracic sclerite. Because, for the most part, this confused condition exists among the Brachycera, attention is called to it. This is the case in all the families except the Stratiomyiidae (Plate XV, 19), the Empididae (Plate, XVIII, 30), the Lonchopteridae (Plate XIX, 31), and the Phoridae (Plate XIX, 32).

Perhaps one of the clearest characters that nature has supplied in the area studied, and one on which the whole group of flies can be divided, is the pleural suture of the mesothorax. In the Nemocera with the exception of the Psychodidae, and in the Brachycera with the exception of the Cyrtidae, this suture runs more or less straight from the coxa to the wing process. If it bends forward at all it is on a rather easy curve, but in all the Brachycera of the Orthorrhapha, with the exception of the one cited above, and in all the Cyclorrhapha, this suture takes an abrupt turn cephalad (in some cases the angle is equal to 90° or more) in its course from the leg to the wing area.

Lastly, the writer wishes to call attention to the presence of a tongue-like structure in the membrane of the mesothoracic coxae of all the Calyptratae and the Acalyptratae, with the exception of the Oestridae, and its absence in all other families except the Syrphidae.

These characteristics do not as a whole point to the same places for the division of the order as the one adopted in this paper, or to any other single classification. But there are characters, such as the presence or absence of the adventitious suture and the character of the pleural suture of the mesothorax, which divide rather definitely where they strike and should be of value for that reason. Certainly this investigation has emphasized the fact that the last word has not been said on the systematic position of some members in such families as the Cyrtidae, the Oestridae, the Scatophagidae, the Ephydridae, the Oscinidae, and a number of others whose study has offered obstructions to uniformities within a time-honored system.

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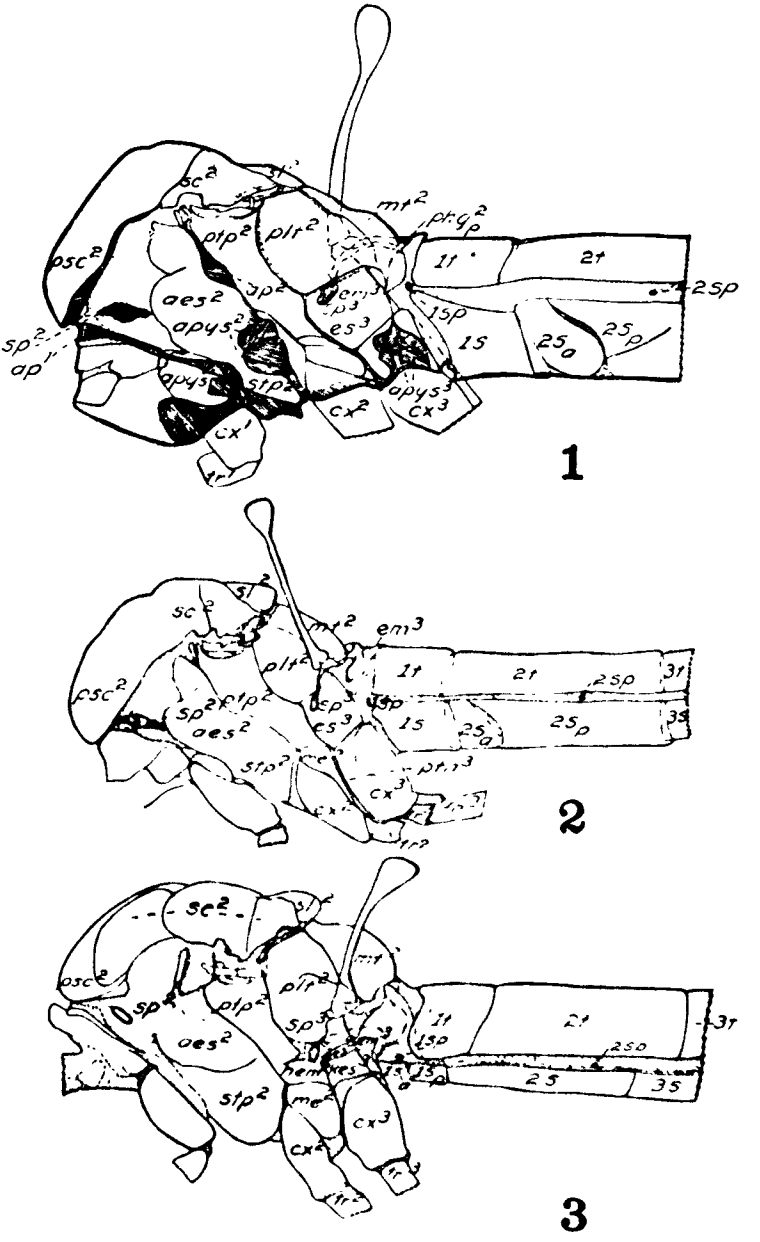
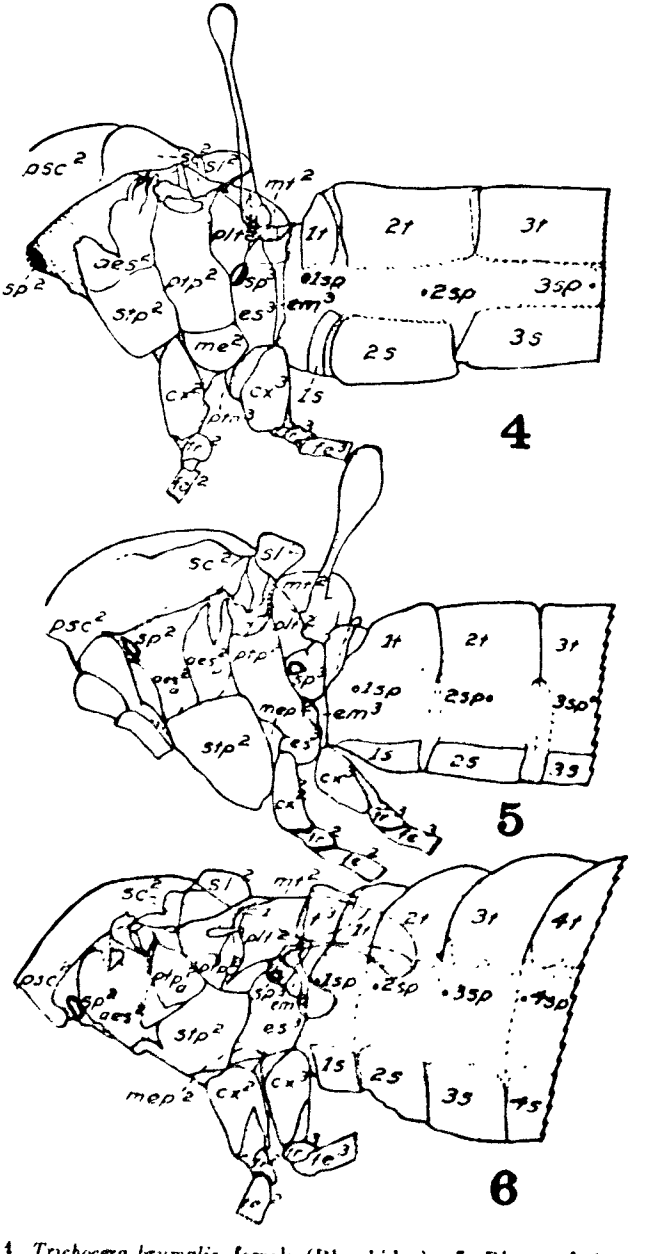
Character Summary Chart

Key
+ Yes — No
? Uncertain

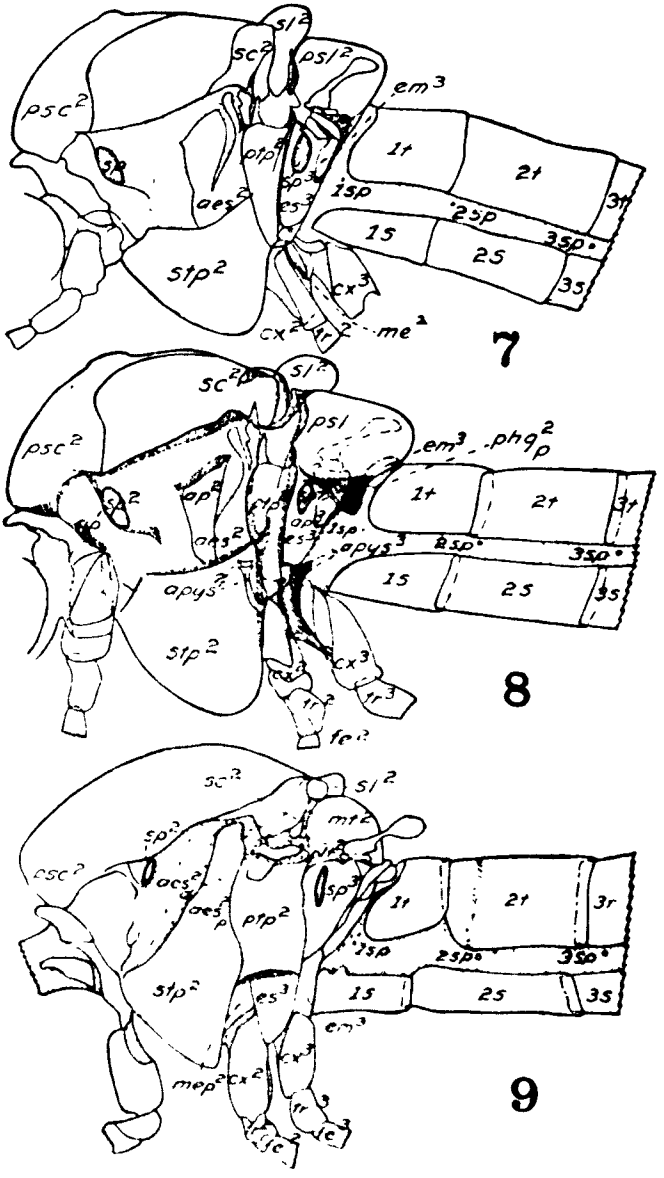
	Sub Group order	Nemocera											
	Sex	♀	♂	♀	♀	♀	♂	♂	♀	♀	♀	♂	♂
	Species	*Pedicia albivitta*	*Pachyrrhina ferruginea*	*Trichocera brumalis*	*Dixa modesta*	*Psychoda sloanei*	*Chironomus ferruginearilla*	*Culex canadensis*	*Anopheles quadrimaculata*	*Corethra albipes*	*Leia winthemi*	*Sciara ochrolabis*	*Rhabdophaga strobiloides*
	Family	Tipulidae	Tipulidae	Rhyphidae	Dixidae	Psychodidae	Chironomidae	Culicidae	Culicidae	Culicidae	Mycetophilidae	Sciaridae	Cecidomyiidae
Mesothoracic pleural suture making an abrupt bend forward in its course from coxa to wing process		—	—	—	—	+	—	—	—	—	—	—	—
Tongue-like structure present in membrane of mesothoracic coxa (cx^2)		—	—	—	—	—	—	—	—	—	—	—	—
Metathoracic pleurotrochantin (ptn^2) present as a chitinized sclerite		?	—	?	—	—	—	—	—	—	—	—	—
Thoracic and abdominal sclerites clearly differentiated		+	+	+	+	—	+	+	+	—	+	+	+
Adventitious suture present in first abdominal tergite		—	—	—	—	—	—	—	—	—	—	—	—
Suture between first and second abdominal tergites present entire		+	+	+	+	+	+	+	+	+	+	+	+
First abdominal tergite subdivided (s) or membranous (m)		—	—	—	—	—	—	—	—	—	—	s	—
Second abdominal tergite subdivided (s) or membranous (m)		—	—	—	—	—	—	—	—	—	—	—	—
First abdominal sternite subdivided (s) or membranous (m)		—	s	—	—	—	—	—	m	—	—	—	—
Second abdominal sternite subdivided (s) or membranous (m)		s	—	—	—	—	—	—	—	—	—	—	—
First abdominal spiracle in membrane		+	+	+	+	+	+	+	+	+	+	+	+
Second abdominal spiracle in membrane		+	+	+	+	+	+	+	+	+	+	+	+
Third abdominal spiracle in membrane		+	+	+	+	+	+	+	+	+	+	+	+
Fourth abdominal spiracle in membrane		+	+	+	+	+	+	+	+	+	+	+	+
Fifth abdominal spiracle in membrane		+	+	+	+	+	+	+	+	+	+	+	+
Number of abdominal spiracles		8	7	7	7	7	7 or 8	7	7	7	7	7	7



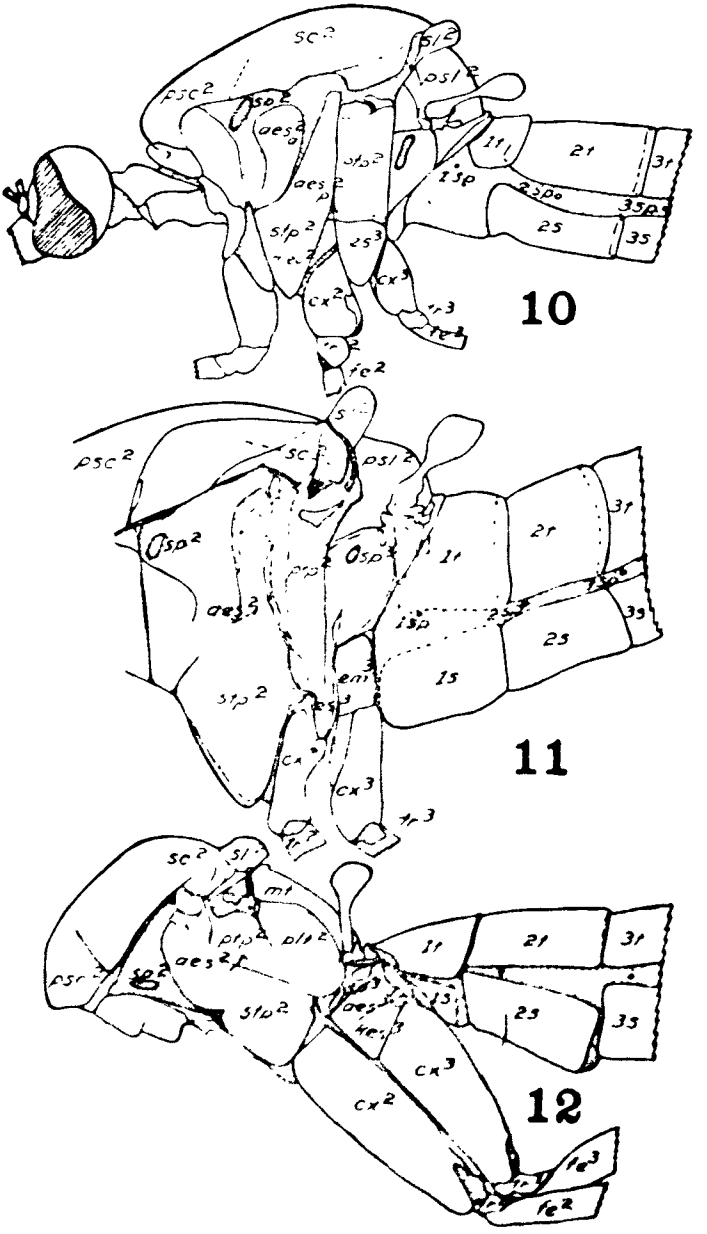
1, *Pedicia albivitta*, female (Tipulidae); internal view, showing endothorax. 2, *Pedicia albivitta*, female (Tipulidae). 3, *Pachyrrhina ferruginea*, male (Tipulidae)



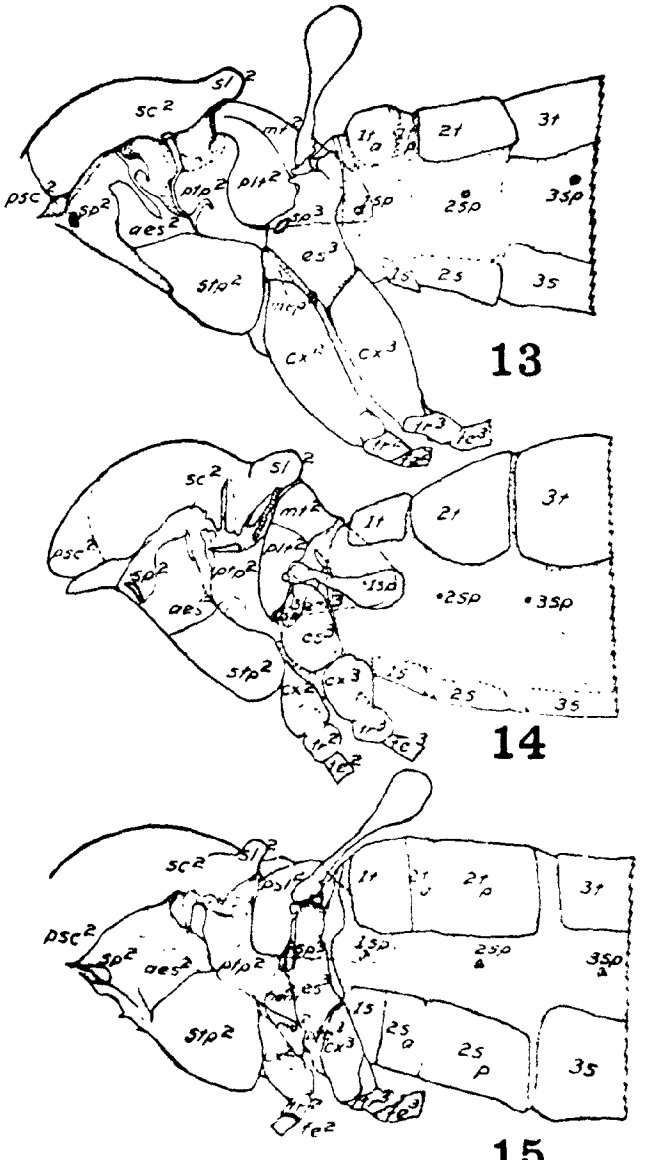
4. *Trichocera hiemalis*, female (Rhyphidae). 5. *Dixa modesta*, female (Dixidae). 6. *Psychoda alosiana*, female (Psychodidae)



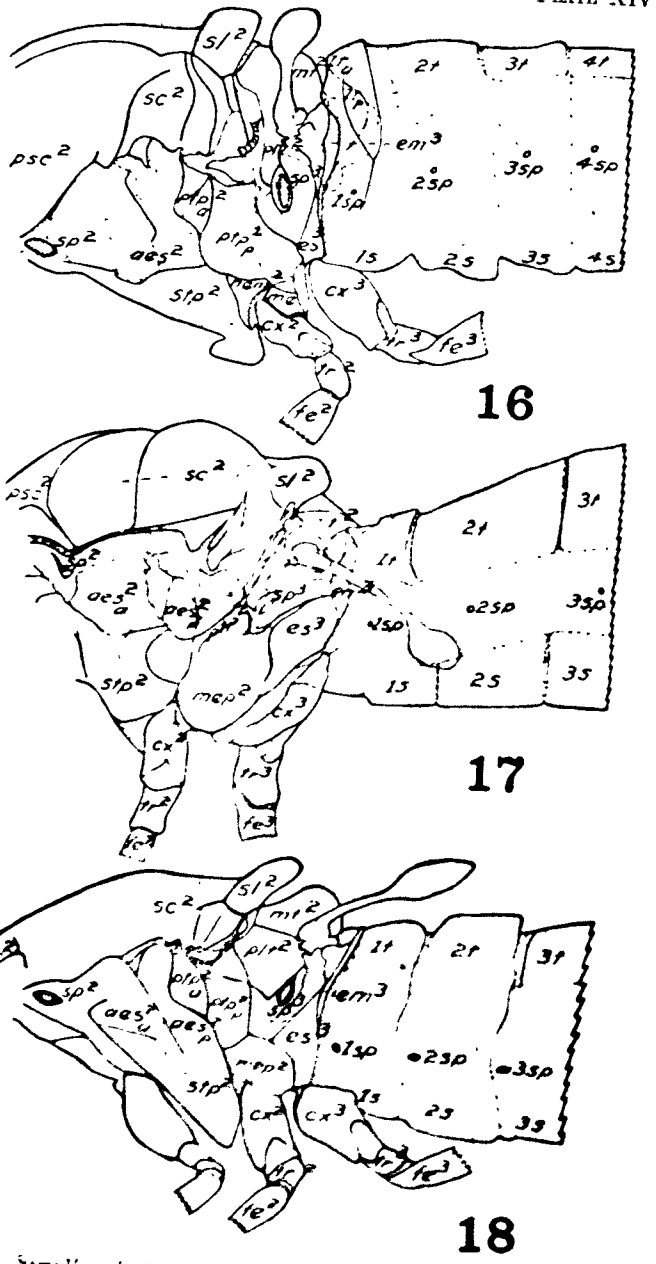
7, *Chironomus ferruginearitta*, male (Chironomidae). 8, *Chironomus ferruginearitta*, male (Chironomidae); internal view, showing endothorax. 9, *Culex canadensis*, male (Culicidae)



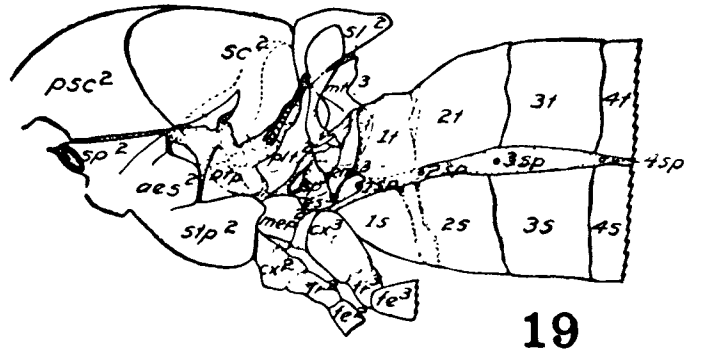
10. *Anisotoma quadrimaculata*, female (Cholevidae). 11. *Corethra albipes*, female (Culicidae). 12. *Leia trianthemi*, female (Mycetophilidae).

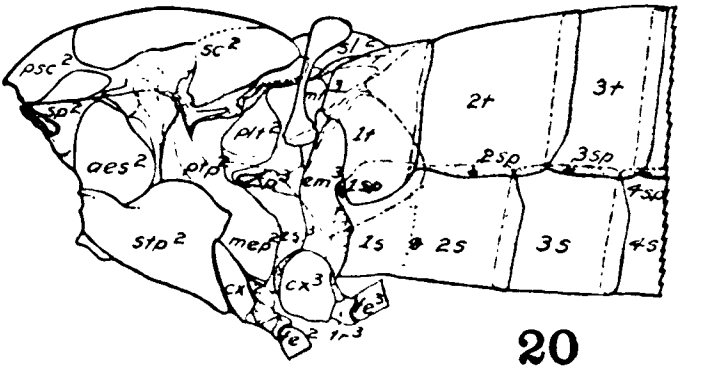


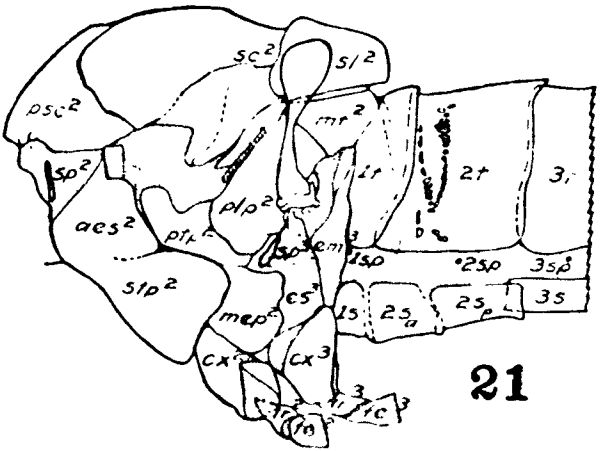
13, *Sciara ochrolabis*, male (Sciaridae). 14, *Rhabdophaga strobiloides*, male (Cecidomyiidae). 15, *Plecia lateroptera*, female (Bibionidae)



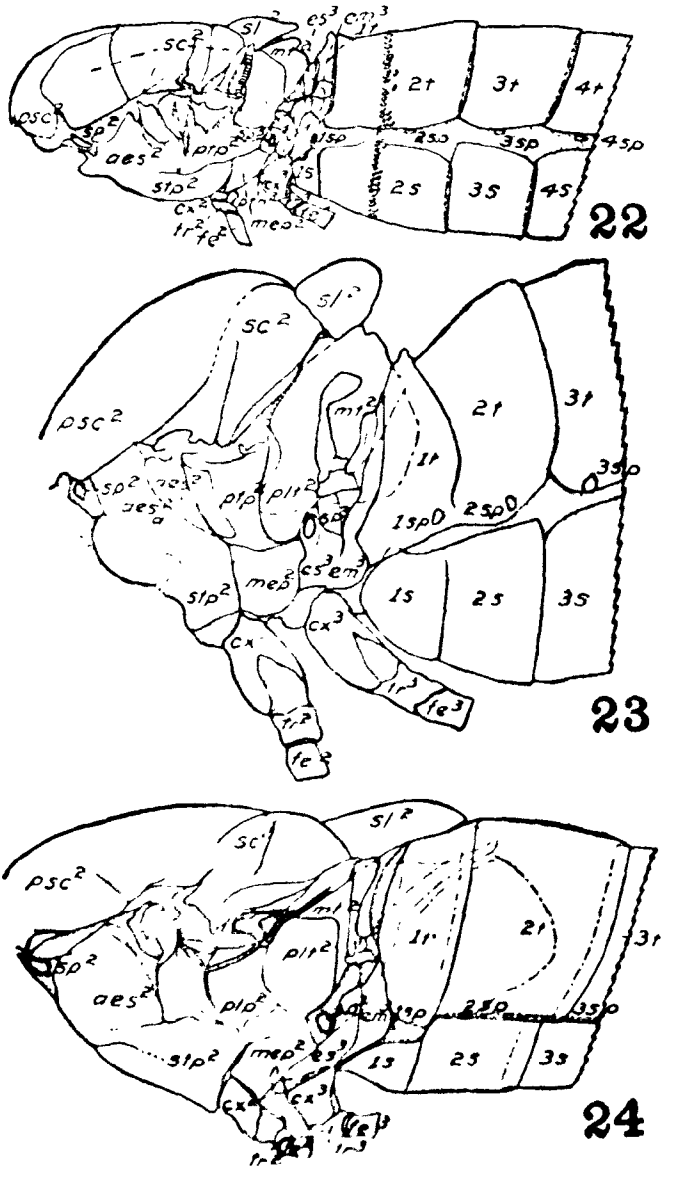
16, *Simulium hirtipes*, male (Simuliidae). 17, *Blepharocera tenuipes*, female (Blepharoceridae). 18, *Orphnephila americana*, female (Orphnephilidae)



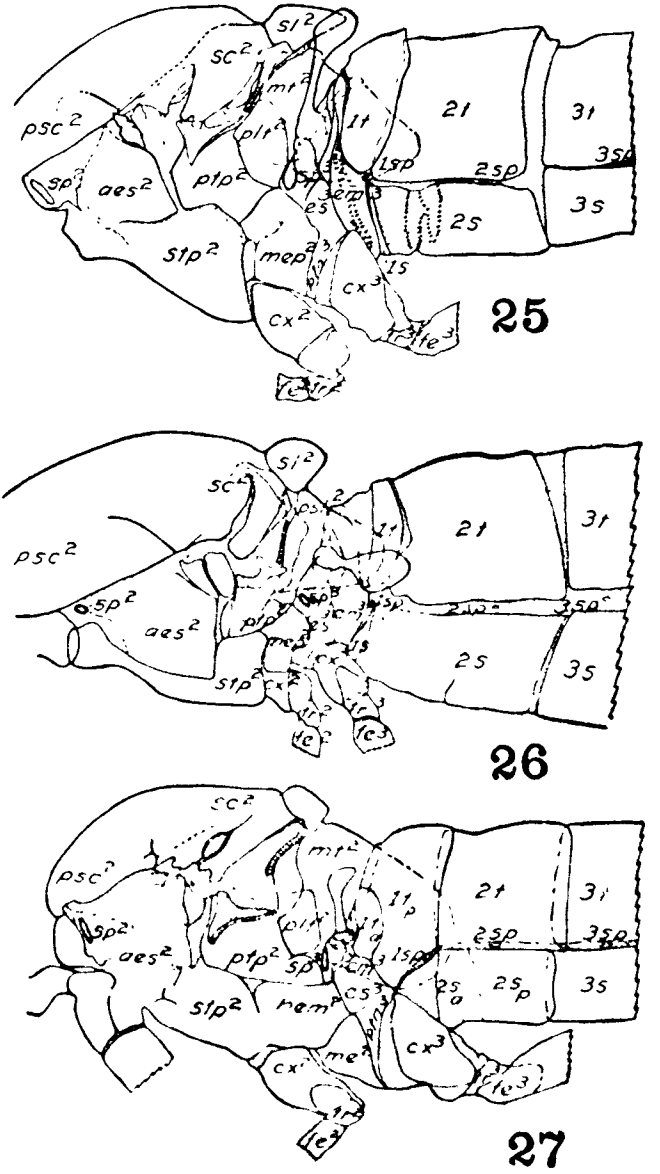




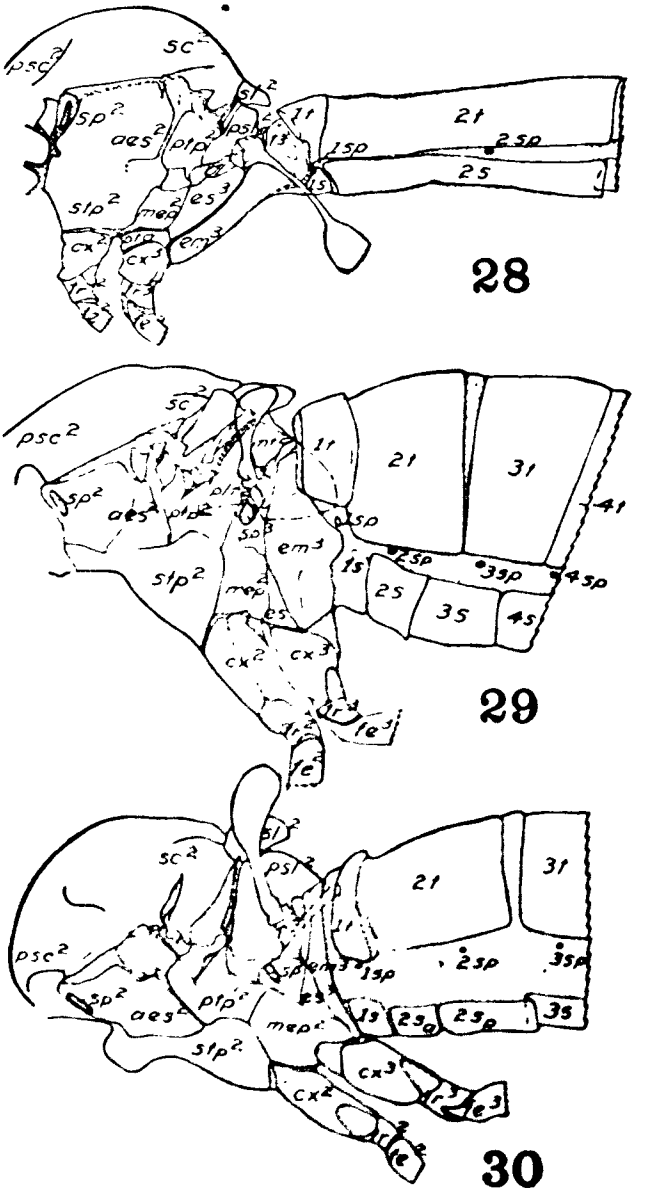
19, *Allognosta fuscitarsis*, female (Stratiomyiidae). 20, *Chrysops indus*, male (Tabanidae). 21, *Chrysopila ornata*, male (Leptidae)



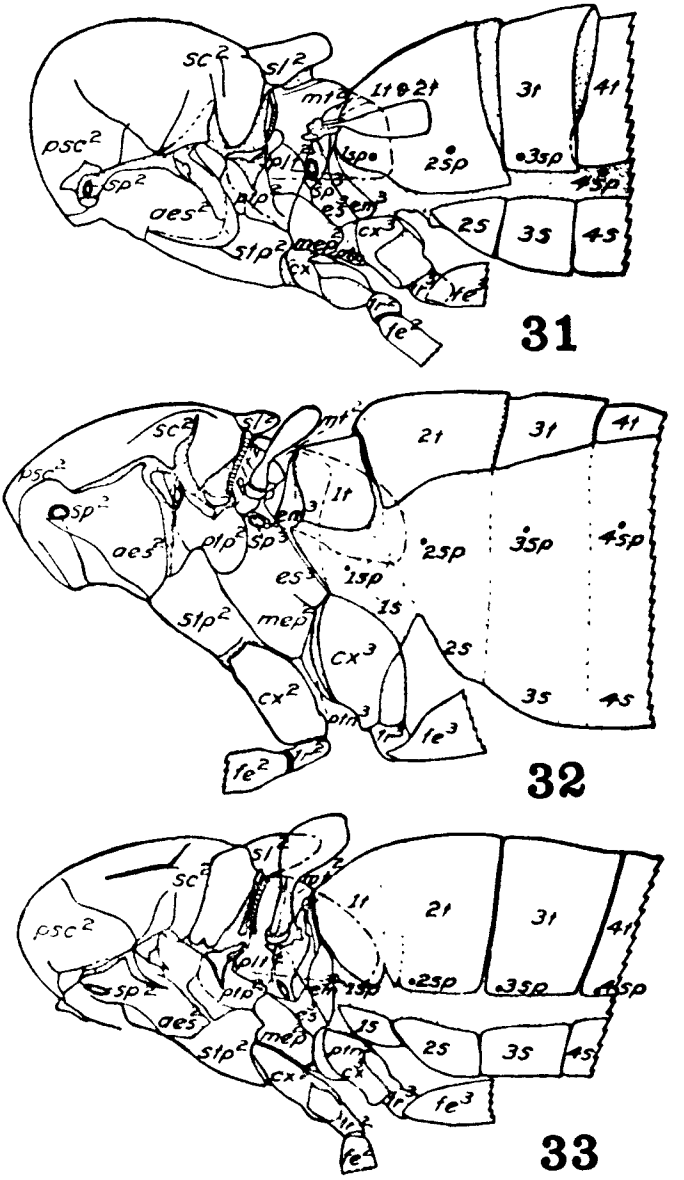
22. *Harmoneura* sp., female (Nemestrinidae). 23, *Oncodes incultus*, female (Cyrtidae). 24, *Anthrax alternata*, female (Bombylidae)



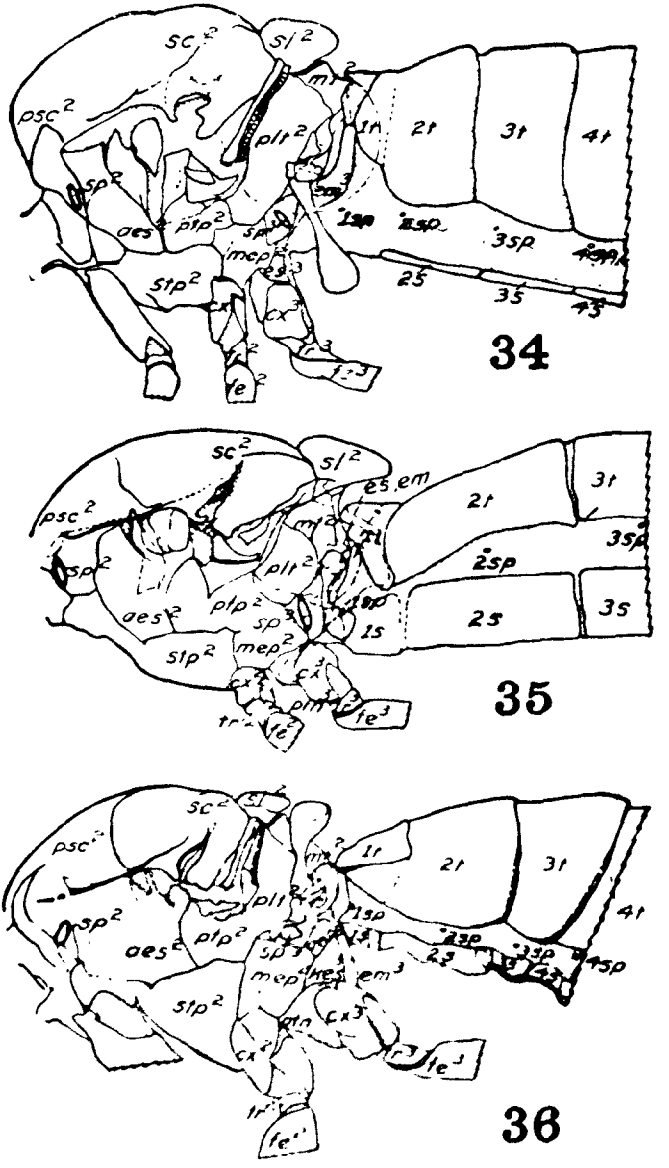
25, *Therera fucata*, male (Thereviдae). 26, *Scenopinus fenestralis*, female (Scenopinidae). 27, *Midas clavatus*, female (Midaidae)



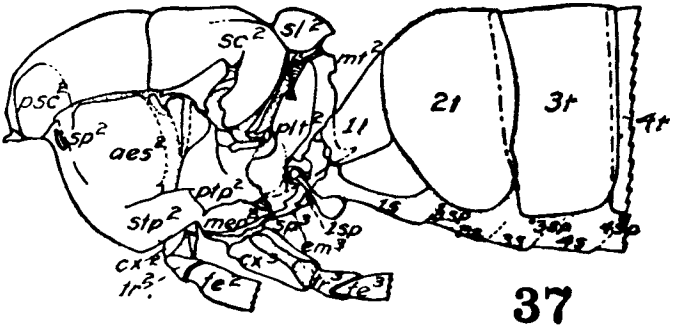
28, *Leptogaster lacer*, female (Asilidae). 29, *Dolichopus cuprinus*, male (Dolichopodidae). 30, *Rhamphomyia* sp., female (Empididae)

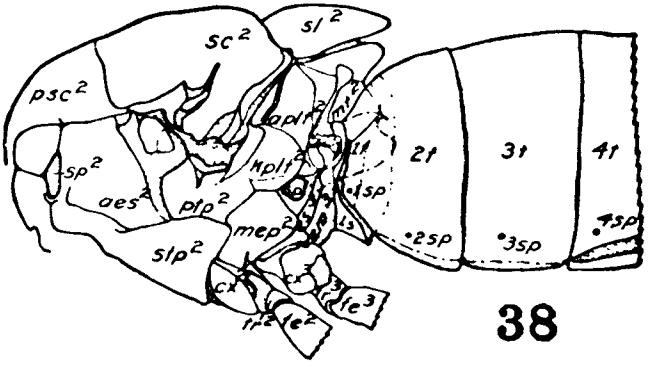


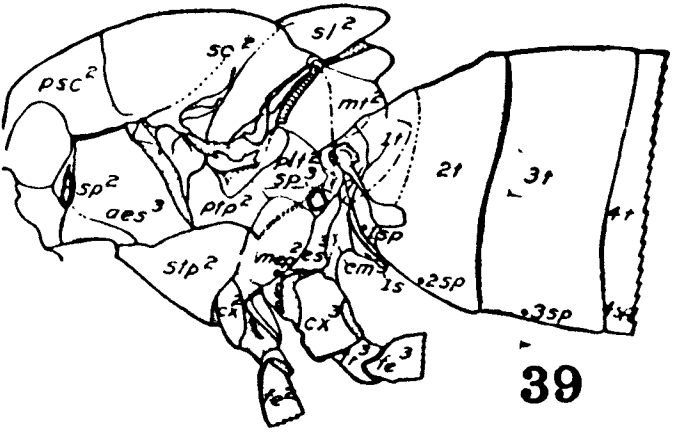
31, *Lonchoptera* sp., female (Lonchopteridae). 32, *Phora concinna* female (Phoridae). 33, *Platypeza velutina*, female (Platypezidae)



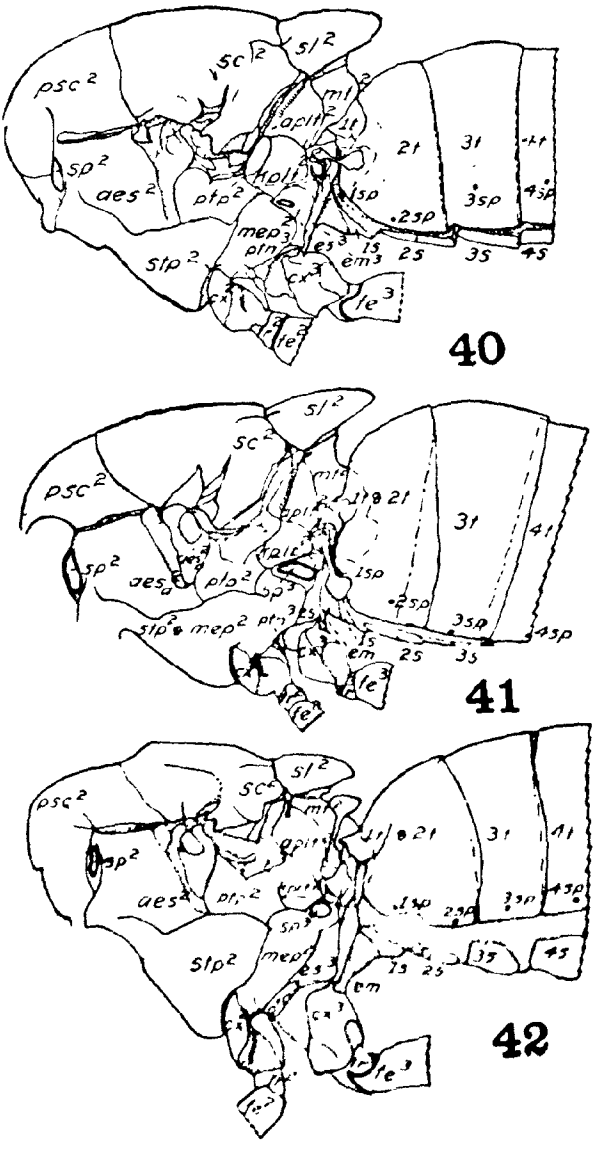
34, *Pipunculus atlanticus*, female (Pipunculidae). 35, *Syrphus americanus*, male (Syrphidae). 36, *Myopa vesiculosa*, male (Conopidae).



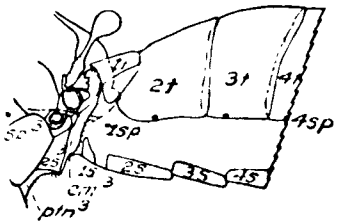




37, *Gastrophilus intestinalis*, female (Oestridae). 38, *Tachina mella*, female (Tachinidae). 39, *Thelaira nigripes*, male (Dexiidae)



40, *Sarcophaga [illegible]*, male Sarcophagidae. 41, *Muscina stabulans*, female Muscidae. 42, *Mesembrius aurulus*, male Anthomyiidae.



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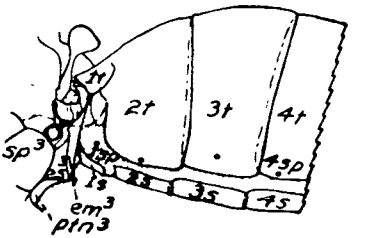

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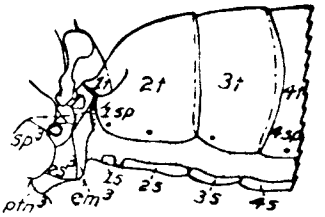

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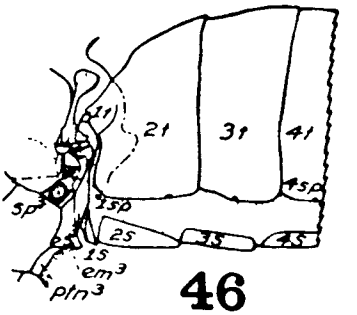

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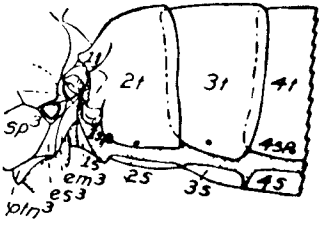

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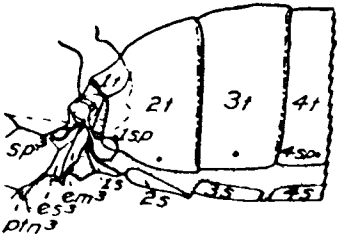

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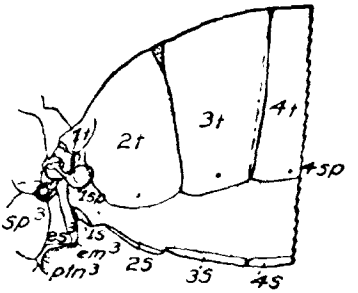
13, *Chortophila ciliicrura*, male (Anthomyiidae). 14, *Hylephila paludis*, female (Anthomyiidae). 15, *Schoenomyza dorsalis*, female (Anthomyiidae). 16, *Ophyra cucullata*, male (Anthomyiidae). 17, *Lispa sociabilis*, female (Anthomyiidae). 18, *Limnophora aequifrons*, male (Anthomyiidae)



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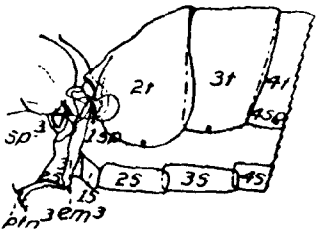

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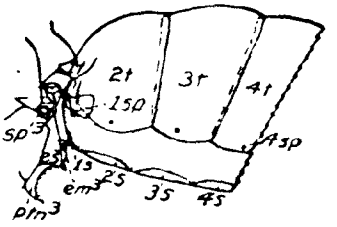

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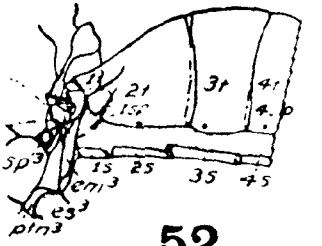

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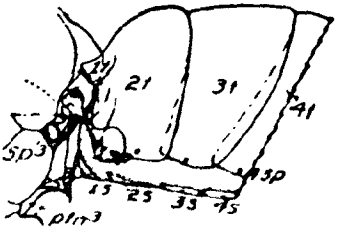

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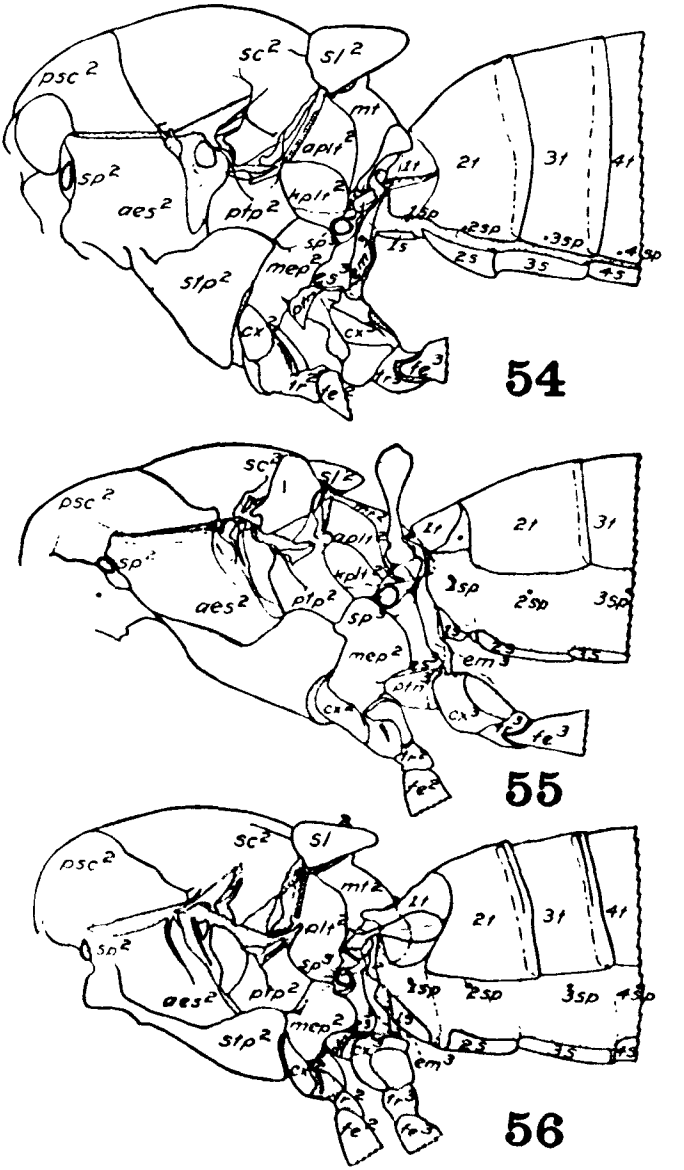
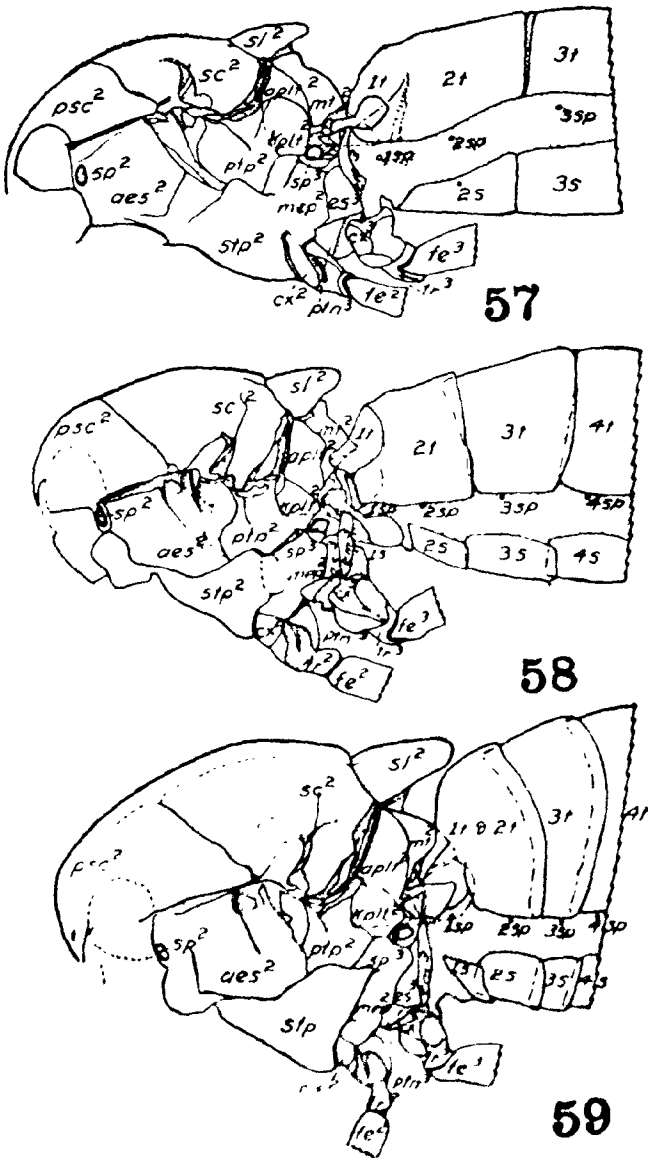
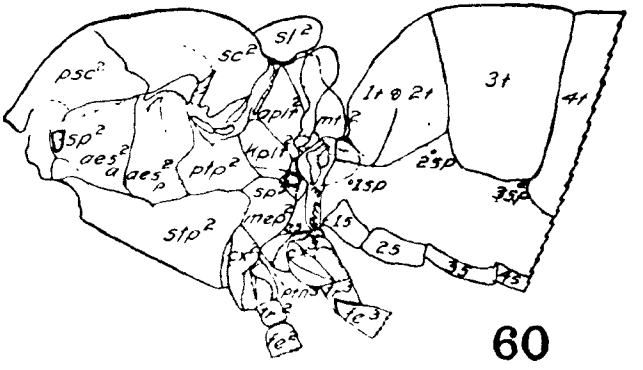
49, *Eremomyia cylindrica*, female (Anthomyiidae). 50, *Pegomyia affinis*, female (Anthomyiidae). 51, *Hylemyia lipara*, female (Anthomyiidae). 52, *Anthomyia radicum*, male (Anthomyiidae). 53, *Hebecnema umbratica*, female (Anthomyiidae).



54, *Scatophaga stercoraria*, male (Scatophagidae). 55, *Clusia lateralis*, female (Heteroneuridae). 56, *Leria serrata*, male (Helomyzidae)



57, *Barbara equicrus* (female, Borboridae); 58, *Ineta umbrarum*, female (Sciomyzidae); 59, *Sapromyza lapulina*, male (Sapromyzidae).



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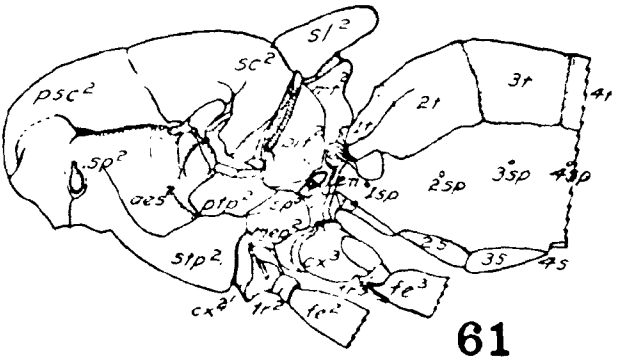

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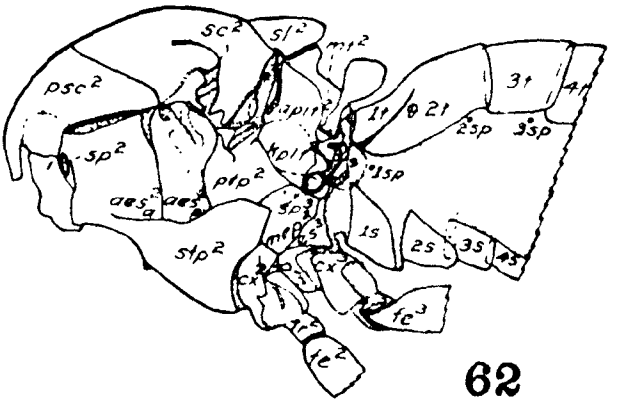

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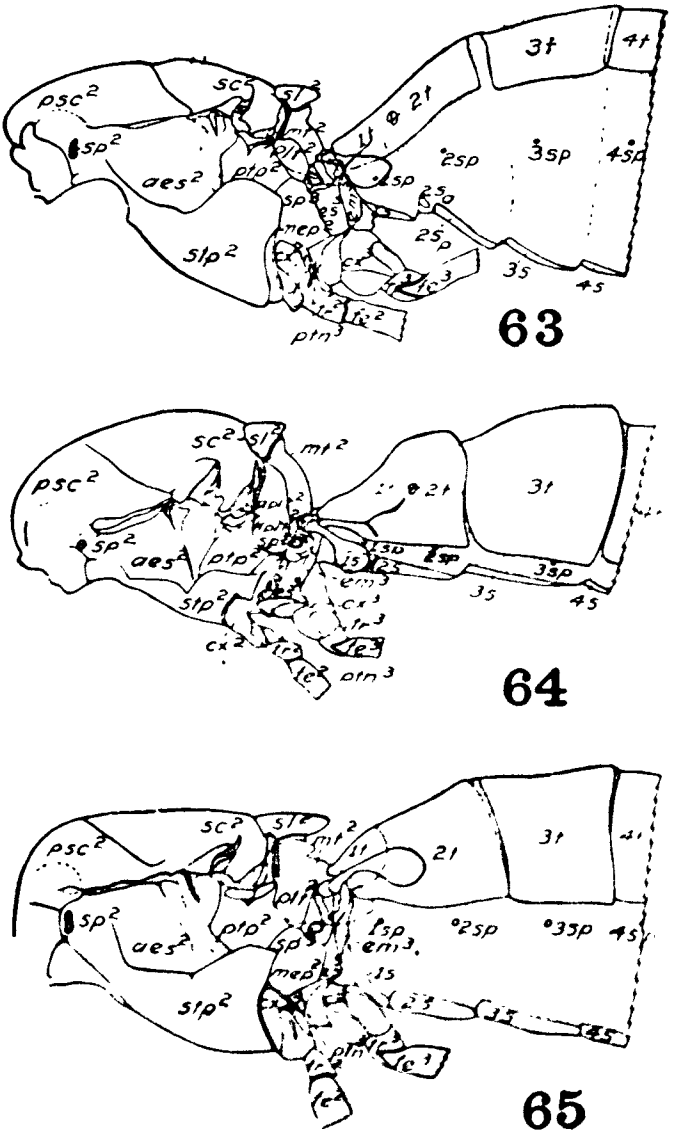
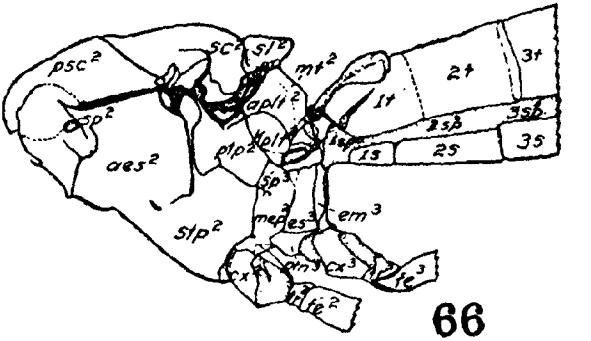
(60, *Rivellia viridulans*, female (Ortalidae). 61, *Rhopalomera flaviceps*, female (Rhopalomeridae). 62, *Euaresta festiva*, female (Trypetidae)



63. *Calobata albiceps*, female (Micropezidae). 64. *Sepsis violacea*, female (Sepsidae). 65. *Prophila aceri*, female (Piophilidae)



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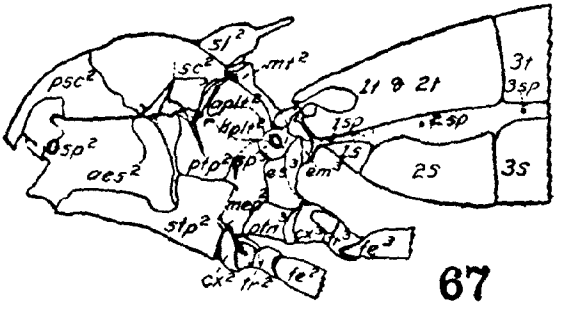

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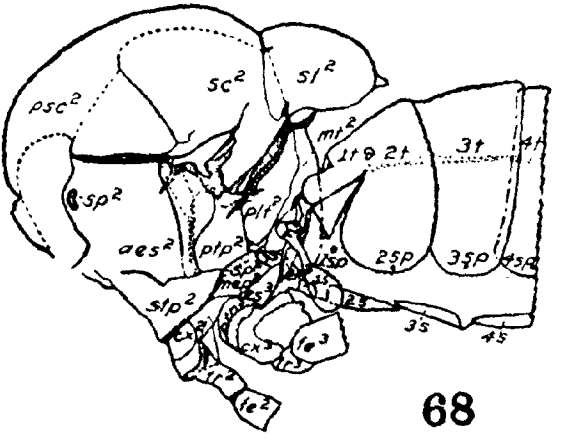

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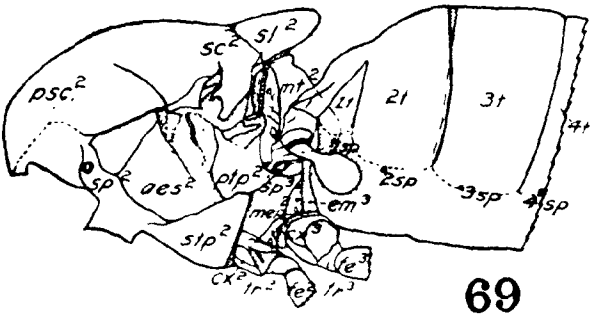
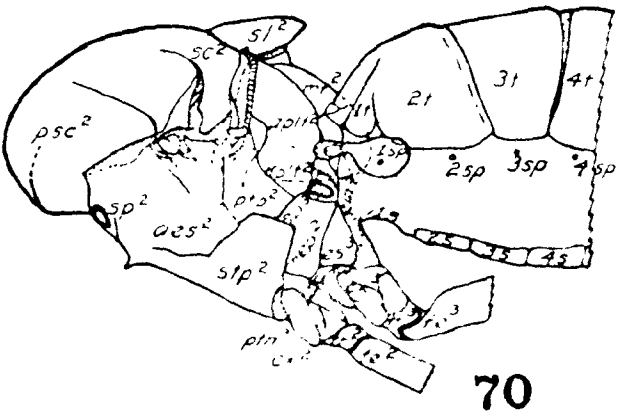
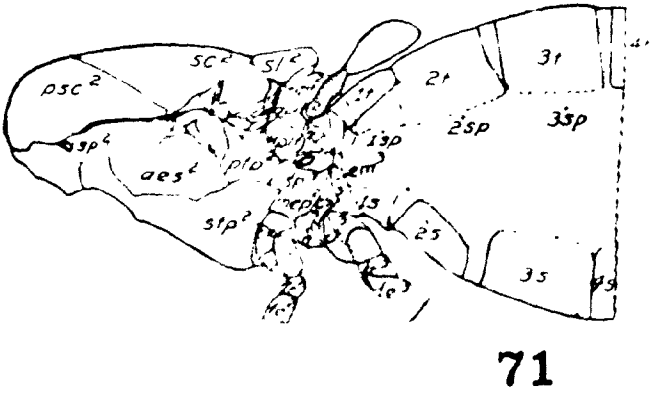
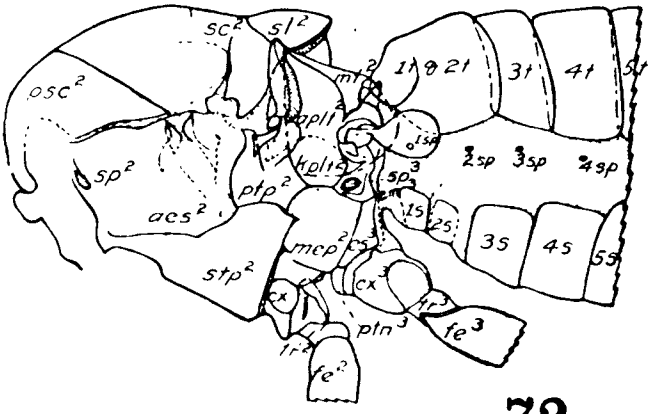
66, *Loxocera pleuritica*, male (Psilidae). 67, *Sphyracephala brevicornis*, female (Diopsidae). 68, *Parydra limpidipennis*, female (Ephydridae)







60. *Chloropsis* sp., male. Oscinidae. 70. *Drosophila melanogaster*, female. Drosophilidae. 71. *Lethomyza gracilis*, female. Geomyzidae.



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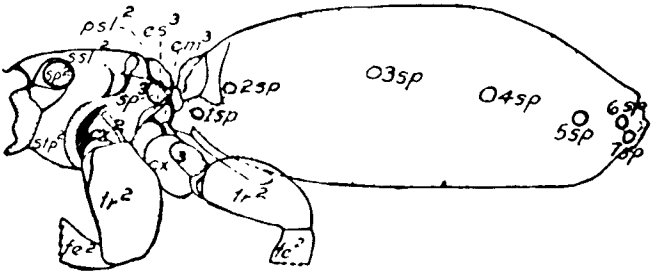

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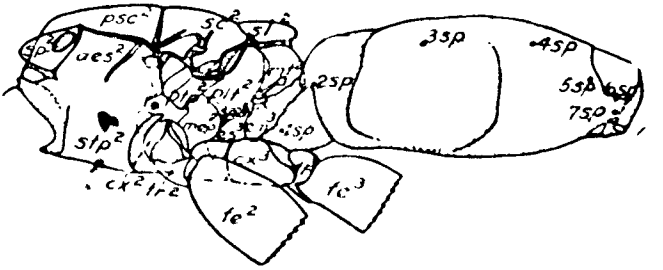

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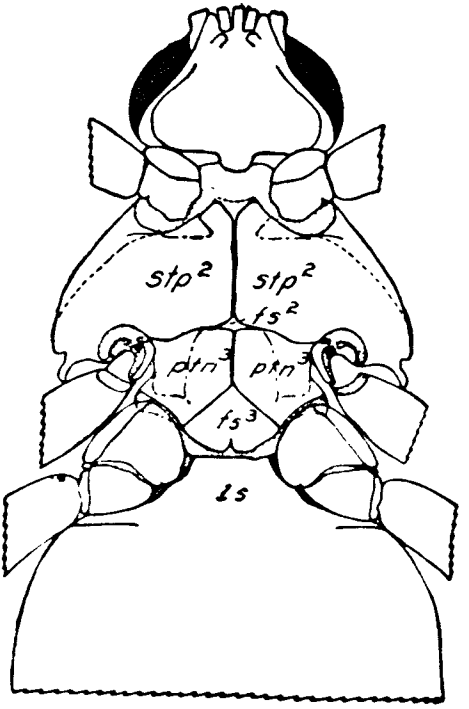
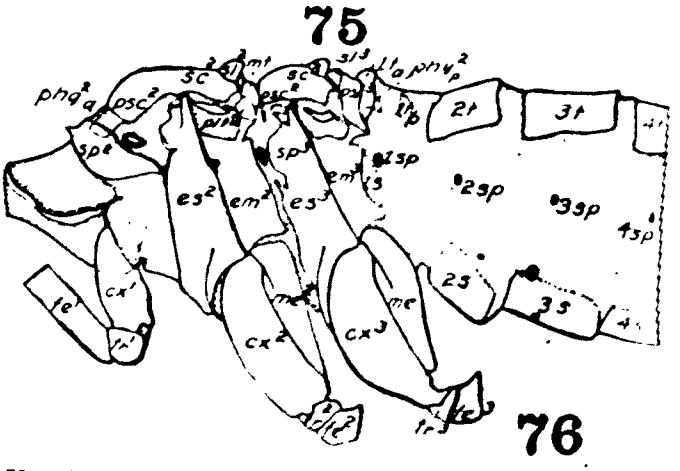
72, *Agromyza lateralis*, male (Agromyzidae). 73, *Melophagus ovinus*, female (Hippoboscidae). 74, *Olfersia americana*, female (Hippoboscidae)





75, *Oligoxia americana*, female (Hippoboscidae); ventral view.
76, *Panorpa venosa*, female (Panorpidae)

AUGUST, 1921 MEMOIR 45

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

THE BOTRYTIS BLIGHT OF TULIPS

EDWIN F. HOPKINS

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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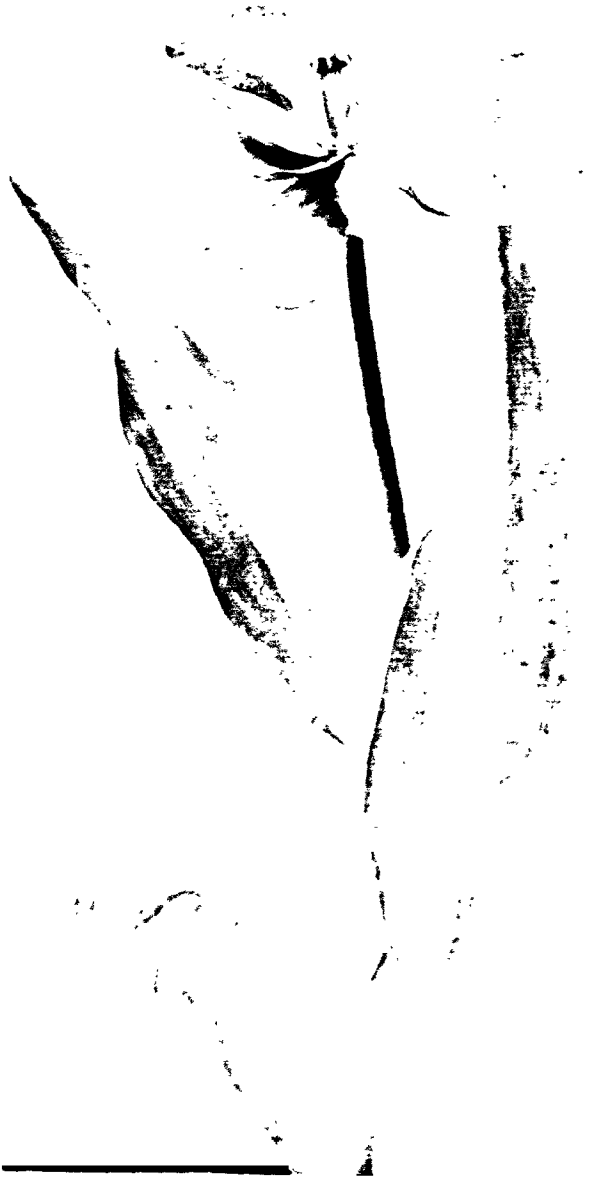
THE BOTRYTIS BLIGHT OF TULIPS



TULIP PLANT AFFECTED WITH BOTRYTIS BLIGHT

THE BOTRYTIS BLIGHT OF TULIPS[1]

EDWIN F. HOPKINS

THE HOST PLANTS

It is reasonably certain that the Botrytis blight is restricted to plants in the genus Tulipa. This genus includes *Tulipa Gesneriana* L., the Darwin, or late, tulips, *T. suaveolens* Roth., the Duc van Thol tulip, embracing the early and forced varieties, and *T. sylvestris* L., the so-called wild tulip. The members of this genus have been under cultivation for so long that it is difficult to refer them to any natural species although the arrangement just given is commonly accepted (Bailey, 1917: 3393-3394).[2]

Numerous references to the occurrence of this disease on other hosts have appeared in the literature. However, most of these statements are based on insufficient evidence, and show that the author had under consideration another Botrytis disease and did not attempt to verify his conclusions by cross inoculations. Ritzema Bos (1903a: 20), for instance, says that while the disease affects other bulbs, such as hyacinths, gladioli, and certain iris species, the tulip is by far the most susceptible. Klebahn (1905: 15-17) takes exception to this statement since he has found the disease on none of these plants except the tulip; furthermore, his experiments show the hyacinth to be immune. He seems to infer that Ritzema Bos was confusing two different diseases, and that possibly, on these hosts, the disease with which he was dealing was caused by *Sclerotium Tuliparum* Klebahn. However, Klebahn states that practical gardeners have told him that on ground which had borne bulbous begonias and dicentra no tulips came up.

Other notes frequently appear by authors who evidently confuse diseases caused by other species of Botrytis with the one under consideration, which is caused by *Botrytis Tulipae* (Lib.) comb. nov. Halsted (1891: 352) gives a good example of this in attributing the disease on onions to this organism.

---

[1] Also presented to the Faculty of the Graduate School of Cornell University, March, 1920, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

ACKNOWLEDGMENT. The author wishes to express his thanks to Professor H. H. Whetzel, of Cornell University, for his many valuable suggestions and for his helpful advice during the progress of the work.

[2] Dates in parenthesis refer to *Bibliography*, pages 359 to 361.

In order to gain some knowledge of the host range of the parasite concerned, numerous cross-inoculations were made by the writer. These experiments, which are summarized under the heading *Pathogenicity* (page 339), prove that the organism concerned does not attack certain of these hosts under artificial conditions, and therefore it probably would not under natural ones. Klebahn (1904, 1905, 1907) had previously made certain cross-inoculations tending to disprove the existence of a generalized type of parasitism in this pathogene.

The disease is restricted, under normal conditions, to the genus Tulipa; and while similar Botrytis diseases occur on the other hosts mentioned, and even on the tulip itself, they are not identical with this one.

VARIETAL SUSCEPTIBILITY

Varieties of both the early tulips, *Tulipa suaveolens*, and the late tulips, *T. Gesneriana*, are susceptible. Likewise, as already mentioned, the wild tulip, *T. silvestris*, has been proved susceptible. The writer has collected diseased specimens of many varieties of the first two species and has seen the disease on the wild species.

Klebahn (1905:11), in his experiments, tested five varieties of tulips, presumably early varieties, but finding all susceptible he drew no general conclusion from this result. He thinks it would be desirable to compare the susceptibility of the early and the late species.

The writer found the disease on a large number of varieties of both species, and isolated the causal organism; he also succeeded in artificially infecting both species. He had almost concluded that there was not much difference in susceptibility. But in the spring of 1917, in a garden on the Cornell University campus where there was then a severe outbreak of the disease, one variety of late tulips (Baronne de la Tonnaye), which had certainly been exposed to the infection, showed no evidence of the disease. Up to the present time there has not been an opportunity to test this variety further.

THE DISEASE

NAMES

Various names have been applied to the disease. Ritzema Bos (1903a: 19) incorrectly used the name *kwaden plekken*, a term applied by Dutch bulb growers to soil that will not produce tulips. Later Klebahn (1907:3)

showed that there are various causes of these "bad spots," but that usually they are due to *Sclerotium Tuliparum*. Hence the term *kwaden plekken* may not be applied specifically to this disease.

Ritzema Bos (1903a:19) uses also the word *Umfallen* to designate the disease as it occurs on tulip tops because it often causes the stem to break over. The writer believes, however, that this name is better applied to a physiological disease of tulips described by Sorauer (1903:265). "Tulip mould" is the term used by Massee (1899:158) and also by Halsted (1902:438). Later Jacob (1912) states that it is commonly known as "fire."

The writer would suggest the name *Botrytis blight* for this disease, since it causes a typical blight, and although there is another Botrytis disease of tulips, this is the more important one by far.

HISTORY AND DISTRIBUTION

The Botrytis blight of tulips was probably first described in 1830 by Madame Libert, in connection with an herbarium specimen (Crypt. Ard. No. 36). She evidently observed only the sclerotia. She describes the fungus from the sclerotia as *Sclerotium Tulipae* Libert. From her description it is evident that she had studied the sclerotia of *Botrytis parasitica* Cavara (Saccardo, 1888-89).

The disease was first carefully observed by Cavara (1888), in upper Italy. However, Ritzema Bos (1903a:26) thinks Wakker (1885.22) had the same disease under consideration before Cavara's publication appeared. He called it "tulpenziekte." Ritzema Bos (1903a:25) states that the disease had been known in Holland for more than twenty years, but that he is not certain when it first became seriously destructive there. In 1890 affected tulip bulbs were sent to him from Norway. The work of Ritzema Bos, while in some respects not very accurate, was valuable in that it attracted attention to the importance of the disease. He began his studies in 1896 and published several papers on the subject.

Carruthers (1901:246) notes the occurrence of the disease in Northamptonshire and Cambridge, England, in 1901. It was reported near St. Petersburg in 1911 (Elenkin, 1911). Klebahn (1904:18) mentions its appearance in Hamburg, Germany, in 1902, and in other parts of Germany

later. He has done some of the most important work in clearing up the confusion in regard to the various sclerotial diseases of tulips and their life histories.

The appearance of the disease in America was first recorded by Halsted (1902). He had received in 1901, from a grower at Cape May, New Jersey, a diseased specimen, the bulb of which had originally been obtained from Holland. He stated that the disease had also occurred the previous season (1902:438). Obviously, therefore, it was introduced directly from Holland.

In a letter to Professor H. H. Whetzel, of Cornell University, Professor W. J. Morse, of the Maine Agricultural Experiment Station, mentions some unpublished records of the appearance of the disease at Barrington, Nova Scotia, in 1904, at Cobourg, Ontario, in 1906, and at Cartine, Maine, in 1910. There are also later notes. Professor Whetzel and the writer have received or collected specimens from Amsterdam, Sassenheim, and Aalsmeer, in Holland; from Germany; from Ithaca, McGraw, Garden City, Jamaica, and Brooklyn, in New York State; from Madison, Wisconsin; from Manistee, Michigan; from Washington, D. C.; from Bellingham, Washington; and from Carthage, Missouri. There is no doubt that the disease is widespread throughout the United States and Canada, and it probably will be found wherever tulips are grown.

ECONOMIC IMPORTANCE

There are apparently no exact figures available regarding the amount of damage from the Botrytis blight. Both Ritzema Bos and Klebahn speak of the great loss which this disease occasions to both field growers and florists. In fact, Ritzema Bos (1903:91) was engaged for a time by a growers' association to investigate the disease.

Elenkin (1911) reports that in 1911, near St. Petersburg, Russia, 50 per cent of the tulip crop was destroyed by this and other tulip diseases. A collection and observations made by Whetzel at the New York Botanical Garden in 1916 show the Botrytis blight to have been severe there at that time. Occurrence of the disease is recorded also by Stout (1918 211), and letters and specimens from Dr. David Griffiths indicate that it was very prevalent in the Federal Government's bulb gardens at Bellingham, Washington, in 1917.

In the spring of 1917 the writer observed the disease in an epiphytotic condition. Most of the tulip tops in the ornamental beds in the Cornell University campus were severely attacked. These were late, or Darwin, tulips, and counts made on one variety, Spathulata, showed 100 per cent of the leaves diseased, of which 33 per cent were strongly infected and 67 per cent only slightly. Of the stalks, 98 per cent were diseased, 23 per cent severely and 75 per cent slightly. The bulbs all showed slight infections, but it is uncertain whether these were infections by *Botrytis Tulipae* or by *Penicillium* sp. However, in the variety Spathulata 4.6 per cent of unmistakable Botrytis lesions were found, and in the variety Mrs. Grover Cleveland, 5.2 per cent. The presence of sclerotia in these lesions made identification certain. These were probably lesions from the previous year and they show how small an amount of original inoculum is necessary to produce a severe infection on the tulip tops. Accordingly it is impossible to lay too much emphasis on the selection of clean bulbs. The writer believes that this is the most important disease of the tulip in this country.

SYMPTOMS

On the bulbs

On the brown outer skin, or husk, of the affected bulbs, small black sclerotia may frequently be found, about 1 millimeter in diameter. They appear also on the old, dried, flower stalk of the previous season, which sometimes remains attached to the bulb (fig. 22). The removal of this papery, brown skin often reveals lesions on the outer, white, bulb scale which might otherwise have escaped notice. These lesions vary from deep yellow to brown, are usually circular in outline, and have a definite margin which may be somewhat raised. The central part is ordinarily depressed and may have on its surface small black sclerotia (fig. 23). The lesions are formed sometimes at the apex of the bulb, sometimes at the base, but more often in the region between. Less frequently the sclerotia may appear white, which is due to their immaturity. By removing the outer, fleshy scale and examining its inner side, it will be seen that some of the lesions have penetrated almost to the inner surface. They rarely extend into the scales beneath.

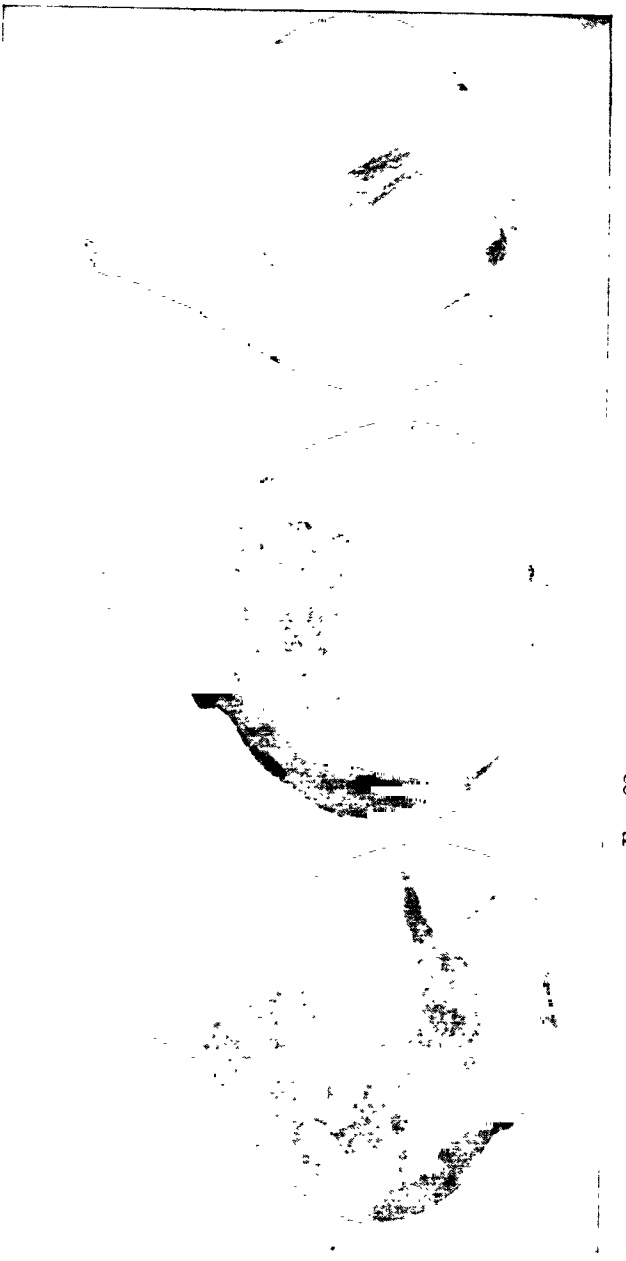


FIG. 22. SCLEROTIA OF BOTRYTIS TULIPAE

Showing them attached to the brown outer skin and the old, dried, flower stalk of dormant bulbs. Natural size

Under warm, humid conditions, a large part of the outer scale may become affected, and in some cases it is so densely covered with sclerotia that these coalesce and form a crust.

Care must be exercised not to confuse the lesions on the bulbs due to the very common Penicillium rot with those caused by *Botrytis Tulipae*.

FIG. 23. BOTRYTIS BLIGHT LESIONS ON THE BULBS

The lesions in the outer, fleshy, bulb scale are depressed and show sclerotia on their surface. Natural size

This is especially true of the incipient lesions which, in these two diseases, are often found almost impossible to differentiate. In general, the lesions of the Penicillium rot are more indefinite in outline and of a lighter yellow color, are usually raised and uneven, and do not, of course, have sclerotia on their surface. The appearance of green mold, which forms under favorable conditions, is a distinguishing characteristic.

FIG. 21. BOTRYTIS BLIGHT LESIONS ON THE LEAVES
Young lesions. Three-fifths natural size

On the leaves

On the leaves the lesions show first as minute, yellowish spots, somewhat elongate in the direction of the leaf veins and surrounded by a darker,

FIG. 25. BOTRYTIS BLIGHT LESIONS ON THE LEAVES
Lesions of a more advanced stage of development. One-half natural size

water-soaked area. They are slightly sunken and give the leaf a speckled appearance. As they enlarge, the areas become more depressed, the

FIG. 26. BOTRYTIS BLIGHT LESIONS ON THE LEAVES
Peculiar twisting of leaves due to a marginal lesion. Natural size

color changes to a whitish gray with a brownish tinge, and a translucent or water-soaked area appears about the margin. At this stage the margins of the lesions are quite definite (fig. 24). Toward the center abundant conidiophores are often produced. Under favorable conditions the lesions enlarge still farther, coalesce, and frequently involve the entire leaf. If a lesion develops toward the base of a leaf, it may cause the leaf to break over. When an infection takes place on the margin of the leaf near the tip, there results the characteristic appearance shown in figure 26. This wrinkling and bending of the leaf to one side is due to the more rapid growth of the healthy tissue opposite the lesion. (Klebahn, 1905:4).

Both young and old lesions are found on the same leaf showing that infections take place continuously (fig. 25). The outer sheathing leaf is likely to be attacked before the others, probably being infected as it emerges from the bulb. It bends downward and usually is abundantly covered with conidiophores (fig. 27).

FIG. 27. A DISEASED PLANT

Showing the outer sheathing leaf infected by contact with a lesion at the tip of the bulb. Note the abundance of conidiophores which give rise to inoculum for secondary infections. Natural size

On the flowers

The lesions on the flowers (Plate XXXIII) are very striking, especially on red varieties of tulips. They begin as minute spots, whitish to light brown, the color being bleached from the perianth. These spots are

FIG. 28. LESIONS ON THE FLOWER
Natural size

evenly distributed over the surface and usually show no Botrytis fructification (fig. 28). After the lesions enlarge, however, they turn a deeper brown and involve the entire segment of the perianth, which finally becomes dry and wrinkled. At this time they show abundant conidiophores. The whole flower may be affected and appear blighted.

FIG. 29. BUD BLIGHT SHOWING THE BLANCHING OF THE INFECTED TISSUE
Natural size

Indeed, this blighting may take place when the flower is still in the bud and prevent it from opening. Such a typical bud blight is reproduced in figure 29.

On the stalks

While the lesions on the stalks are still small, they have much the same appearance as those on the leaves except that they are more elongate and more depressed. They are of a light brownish color in the center, and are surrounded by a water-soaked area. Older lesions near the base of the stalk appear as dark brown patches and often bear sclerotia on their surfaces, while those higher on the stalk, usually originating in the leaf axils, are grayish white and are covered with conidiophores. Both this blanching effect and the conidial layer are well illustrated in figure 30.

The extension of the lesion through the stem causes the latter to weaken at the point of attack and break over. If the lesion is near the base, the whole plant topples over; if it is higher up, the flower droops.

ETIOLOGY

Nomenclature

The tulip disease under discussion is caused by *Botrytis Tulipae* (Libert) comb. nov. A sclerotial form, referred to the form genus Sclerotium by Madame Libert, in 1830, belongs to this species. She called it *Sclerotium Tulipae* and was the first to describe it (Crypt. Ard., no. 36). As previously mentioned, she apparently did not observe the conidial form. Her original description, which the writer has not been able to see, is taken from Klebahn (1907:5) who quotes it as follows:

Sclerotium Tulipae, N. Sparsum, adnatum, parvum, ovale, pallide fuscum, laeve, demum nigrum, rugosum, intus album. Ad caules, pericarpia et semina *Tulipae Gesneranae*. Autumno.

In 1836 the species was again designated as *Sclerotium Tulipae* by Weinmann (1836:647). Sometime between 1841 and 1859 it was once more described in connection with an herbarium specimen, this time by Westendorp. He called it *Sclerotium entogenum* (Herb. crypt. Belg., no. 827). Finally Cavara (1888) described the fungus more completely,

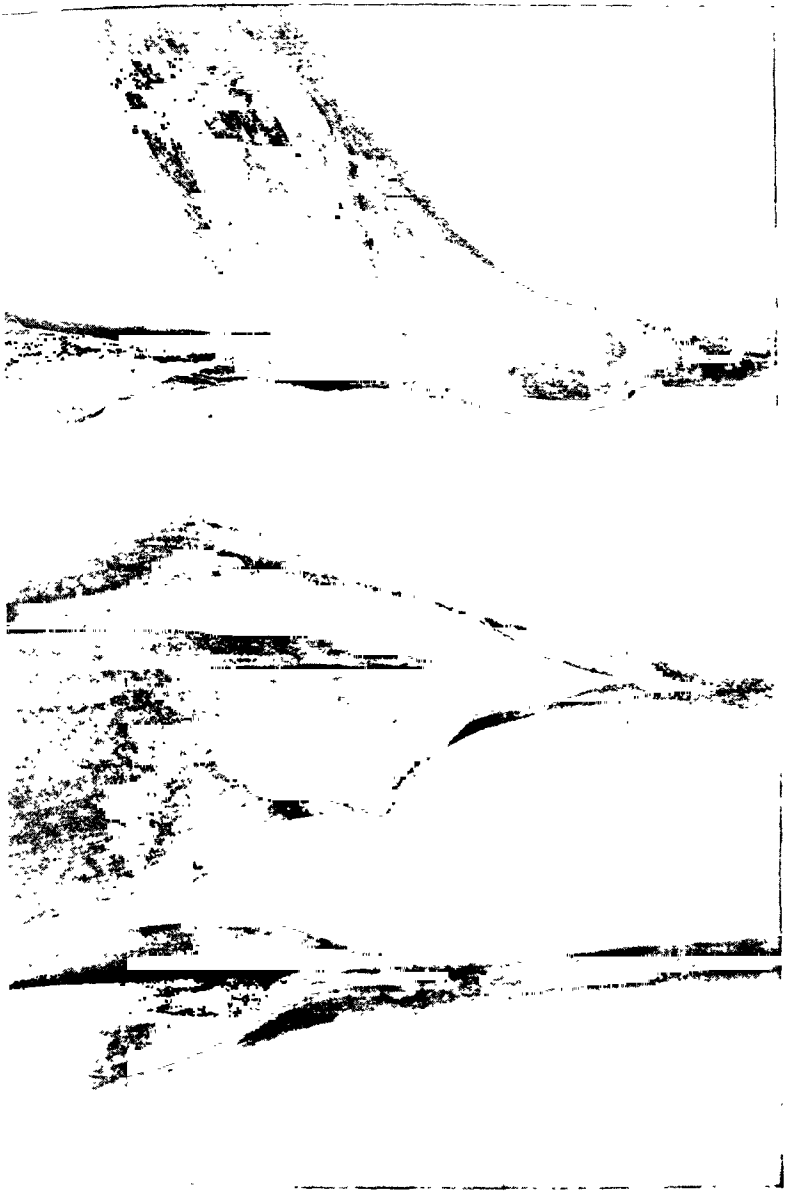


FIG. 30. DISEASED STALKS
Natural size

including both the conidial and the sclerotial stages, which he assumed belonged to the same species. His description is as follows:

Botrytis parasitica nov. sp. Hyphis cinereis sparsis, erectis, articulo basali inflato; conidiis ovatis, magnis, breviter pedicellatis, in ramulis minutis, capitatis, umbellatim dispositis; hyalinis vel dilute cinereis, 16–20 x 10–13 μ.

Forma scleroziale.

Sclerotium Tulipae Lib. Haemisphaericum, vel oblongum, nigrum, vix rugosum, superficiale vel immersum, intus albidum ½–1 mm. latum.

Hab. Ad folia, caules, petala, et capsulas *Tulipae Gesnerianae* in Horto botanico ticinensi.

Cavara (1888:432) justifies his description of this species as a new one on the basis of morphological differences and also because of its strong parasitic action. In his discussion of nomenclature, he says that *Sclerotium Tulipae* Terry, which infects tulips in the south of France, according to Saccardo (1888-89,) is probably a synonym of *Sclerotium cepivorum* var *Tulipae* Desm., and perhaps is the same as *Scl. cepae* Desm. Cavara was not able to compare specimens of *Scl. Tulipae* Terry with *Scl. Tulipae* Lib. The writer, however, had an opportunity to examine a specimen of the former at the herbarium of the New York Botanical Garden. This specimen consists of three or four sclerotia with no adhering plant material. The sclerotia are large, however, and are not those of *Botrytis Tulipae* (Lib.) comb. nov. At the same place the author was able to see some of the collection of Cavara designated *Botrytis parasitica* Cav., and found it to be identical with his own collections.

Massee (1899:383) describes the organism as *Sclerotinia parasitica*. This description was not based on a perfect stage and in Massee's key is placed under "Conodial form only known." Since there is no evidence that the species under consideration is a Sclerotinia, this name is not valid. Massee's description is as follows:

Sclerotinia parasitica, Massee; *Botrytis parasitica*, Cavara. Conidiophores grey, scattered, erect, basal joint inflated; conidia obovate, large, shortly pedicellate, on short umbellately arranged branchlets, hyaline or tinged grey, 16–21 x 10–13 μ; sclerotia formed in the parenchyma of the host, globose-depressed, smooth, greyish, then black, 2–3 mm. diam., sometimes numerous, and forming black crusts.

Botrytis on leaves, stem, and flowers of cultivated tulips; sclerotia more especially on the bulbs.

Distr. Holland, Britain.

A consideration of these facts has led to the following designation of the species:

Botrytis Tulipae (Libert) comb. nov.
Sclerotium Tulipae Lib. Crypt. Ard., no. 36. 1830.
Sclerotium Tulipae Weinn. Hym. Ross., p. 647. 1836.
Sclerotium entogenum West. Herb. crypt. Belg., no. 827. 1841–1859.
Botrytis parasitica Cav. Appunti die Pathologia Vegetale. Ist. Bot. R. Univ. Pavia. Atti 2 1 432. 1888.
Sclerotinia parasitica Massee. A text book of plant diseases, p. 383. 1899.

Botrytis Tulipae (Libert) comb. nov. may be briefly described as follows: Mycelium variable in diameter, often anastomosing, branches not constricted at the base; conidiophores arising directly from the mycelium, erect, brown in color, proliferating, twisting on their axils when dry, slightly swollen at the base; branches of conidiophore arising at an angle of about 60 degrees, dichotomous, not streptiform, apices swollen; conidia large, 12-24 x 10-20 μ, obovate, reddish brown in mass; microscopically gray to hyaline, smooth with a short stalk, often or commonly not remaining attached; sclerotia at first white, finally black, small, 1-2 millimeters in diameter, circular or somewhat elliptical in outline, flattened vertically and often convex. Microconidia globose, about 3 μ in diameter, occurring on special penicillate, obclavate conidiophores arising in white tufts from the substratum (fig. 40) Parasitic on *Tulipa* spp.

Cavara (1888:432) says that *Sclerotium entogenum* West. develops on the stalks of asparagus and does not differ greatly from *Scl. Tulipae* Lib.; he says, moreover, that Westendorp thinks *Sclerotium entogenum* West. should be regarded as the type of the species. *Sclerotium Tuliparum* Klebahn is a species which must not be confused with *Botrytis Tulipae*. It is a large, sclerotial form with which no conidial stage has yet been connected.

The species must, therefore, still be classified among the Hyphomycetes of the Fungi Imperfecti. It is placed there by Lindau (1900:435) in the subgroup Mucedinaceae-Hyalosporae-Botrytideae.

Klebahn (1904:21), from his studies on *B. Tulipae*, seems certain of the connection of the sclerotia occurring on the tulip bulbs with the conidial form on the leaves. However, as he did not use pure-culture methods, it seemed desirable to clear up this point. Pure cultures were made by the writer from the sclerotia occurring on the bulb and from conidia on the leaves of the same tulip plant. These cultures were identical, and when inoculated into sterilized tulip leaves both produced normal conidia and sclerotia. Both also caused infection of healthy tulip plants.

Morphology

The mycelium shows no peculiar characteristics. It varies in diameter, depending on the conditions under which it lives. The branches are not constricted where they join the parent hypha. Anastomosing is frequent (fig. 31).

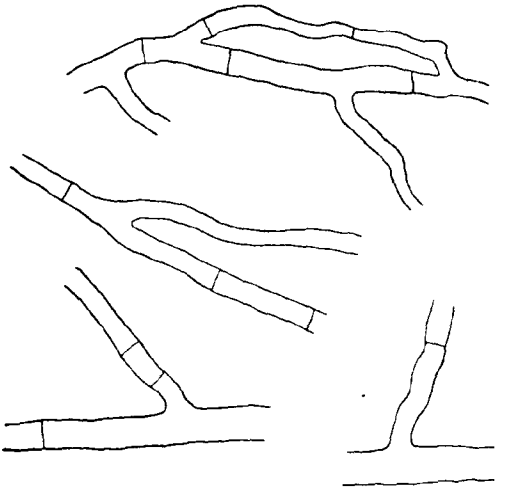


FIG. 31. MYCELIUM OF BOTRYTIS TULIPAE. × 600
Type of branching and anastomosing of the hyphae. (Camera-lucida drawing)

The conidiophores, when mature, are deep brown in color except near the base, where they are hyaline. They are indeterminate in length, for under favorable conditions, after forming one head of conidia terminally, the main axis may proliferate and form another head (fig. 50). This may be repeated until finally there are several clusters of conidia on a single conidiophore (fig. 32). It should be remembered that although some of these clusters appear to be lateral, they are really formed terminally. When

FIG. 32. CONIDIOPHORE OF BOTRYTIS TULIPAE. × 67
A conidiophore unmounted. The several clusters of conidia due to proliferation, and the twisting of the stalk when dry, are both visible. (Camera-lucida drawing)

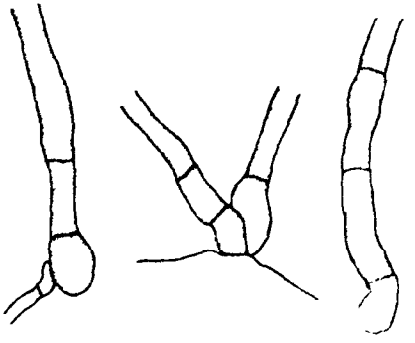


FIG. 33. SWOLLEN BASES OF CONIDIOPHORES OF BOTRYTIS TULIPAE. × 600
(Camera-lucida drawing)

dry, the conidiophore is flattened and twisted on its axis, and is slightly swollen at the base (fig. 33).

The branches of the conidiophore rise from the main stalk at an angle of about 60 degrees, and their ultimate ends, which bear the conidia, are somewhat swollen. The conidia are produced on these swollen ends by a pushing out of the protoplasm in a bud-like manner, but they shortly assume a definite shape. When mature, they remain attached by short sterigmata (figs. 34 and 35). Various stages of conidial formation

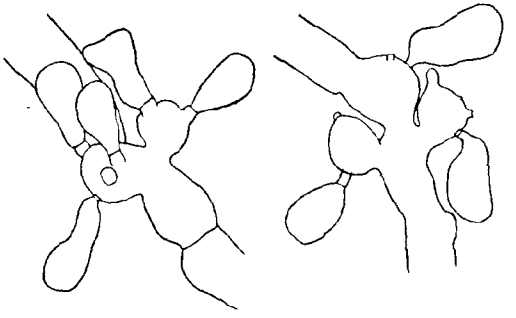


FIG. 34. ATTACHMENT OF CONIDIA OF BOTRYTIS TULIPAE. × 600

Camera-lucida outline of conidia shown in fig. 35. Proliferation of the conidiophore has taken place after the formation of conidia on the head.

FIG. 35. ATTACHMENT OF CONIDIA OF BOTRYTIS TULIPAE. × 840

Note the short sterigma. These conidia are mature. (Photomicrograph)

are shown in figures 36 and 37.[3] Usually young conidiophores were chosen for study because of the firmer attachment of the conidia. The preparation of the mounts required considerable patience because of the delicate attachment of the conidia, and oftentimes many mounts were prepared before one was obtained which showed clearly the details of structure. When young, the conidia are hyaline, but as they mature they assume, in mass, a brownish color. Microscopical examination shows that most of this color is in the spore wall. The conidia are obovate, and when shed, the short sterigmata may sometimes be seen still attached to the spores.

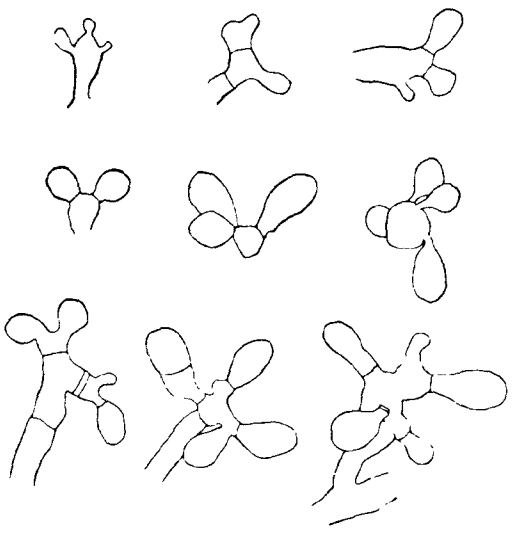


FIG. 36. DEVELOPMENT OF CONIDIA OF BOTRYTIS TULIPAE. × 600

Illustrating the bud-like manner of their formation. (Camera-lucida drawing)

The conidia vary considerably in length and to a less extent in width, but this variation does not depart greatly from a mean which is more or less constant. This is shown graphically in figure 38, which represents the measurements of one hundred spores. One curve expresses the variation of the spore length and the other that of the spore width.

The spores measured were from single-spore cultures and developed on sterilized tulip leaves in petri dishes. Abundant conidial fructifications were formed which were practically identical in appearance with those occurring in nature. They were mounted in the mounting fluid previously described[3] and were measured under the oil-immersion lens by

[3] In studying the detail of the conidiophore, especially the attachment of the conidia, satisfactory mounts were obtained by first adding to the material on the slide a drop of 70-per-cent alcohol in order to "wet" the conidiophores rapidly. The material was then flooded immediately with a mounting fluid prepared by mixing equal parts of 2-per-cent potassium acetate in water and 10-per-cent glycerin in 70-per-cent alcohol and then adding a trace of copper acetate. The excess mounting fluid was removed with filter paper and the mount covered with a cover glass. Such mounts keep very well, do not dry out, and may be kept permanently when ringed with balsam or gold size.

means of camera-lucida drawings. One hundred spores were outlined and the outlines measured with a millimeter rule. The error in measuring was calculated to be less than 2 per cent. On the basis of these measurements the average limits of variation may be placed at 12-24 x 10-20 μ.

These figures do not show the distribution of the spores within these limits. From figure 38, however, it is apparent that the greater number have a length of 16-17 μ and a width of 9-10 μ. These measurements were checked with those of spores from another culture derived from a different locality. Measurements made of the spores of a large number of Botrytis specimens seem to show that one hundred conidia suffice to establish the mode for a given species.

FIG 37 DEVELOPMENT OF CONIDIA OF BOTRYTIS TULIPAE × 600

Mature conidia. (Camera-lucida drawing)

The sclerotia as formed in a petri-dish culture, (fig. 39) are at first white, and later, a shiny black. They are circular, elliptical, or somewhat irregular in outline, flattened vertically, and often slightly convex. They might be described by the term "loaf-shaped." Ordinarily the sclerotia are about one millimeter in diameter. Their size may be considerably affected by the amount of drying to which they are subjected.

Physiology

Growth

Botrytis Tulipae grows very readily on the various kinds of media, both liquid and solid, on which it has been planted. In the writer's experimental work the commonest medium employed was potato-dextrose agar. On this the fungus makes a rapid, fluffy mycelial growth, which later becomes appressed to the surface of the agar and the sclerotia then begin to form. These are very numerous and are imbedded in a tough, mycelial membrane which covers the surface of the substratum. As mentioned under *Conidia production*, conidia are rarely formed in such cultures. Moreover, there is scarcely any color production in this medium.

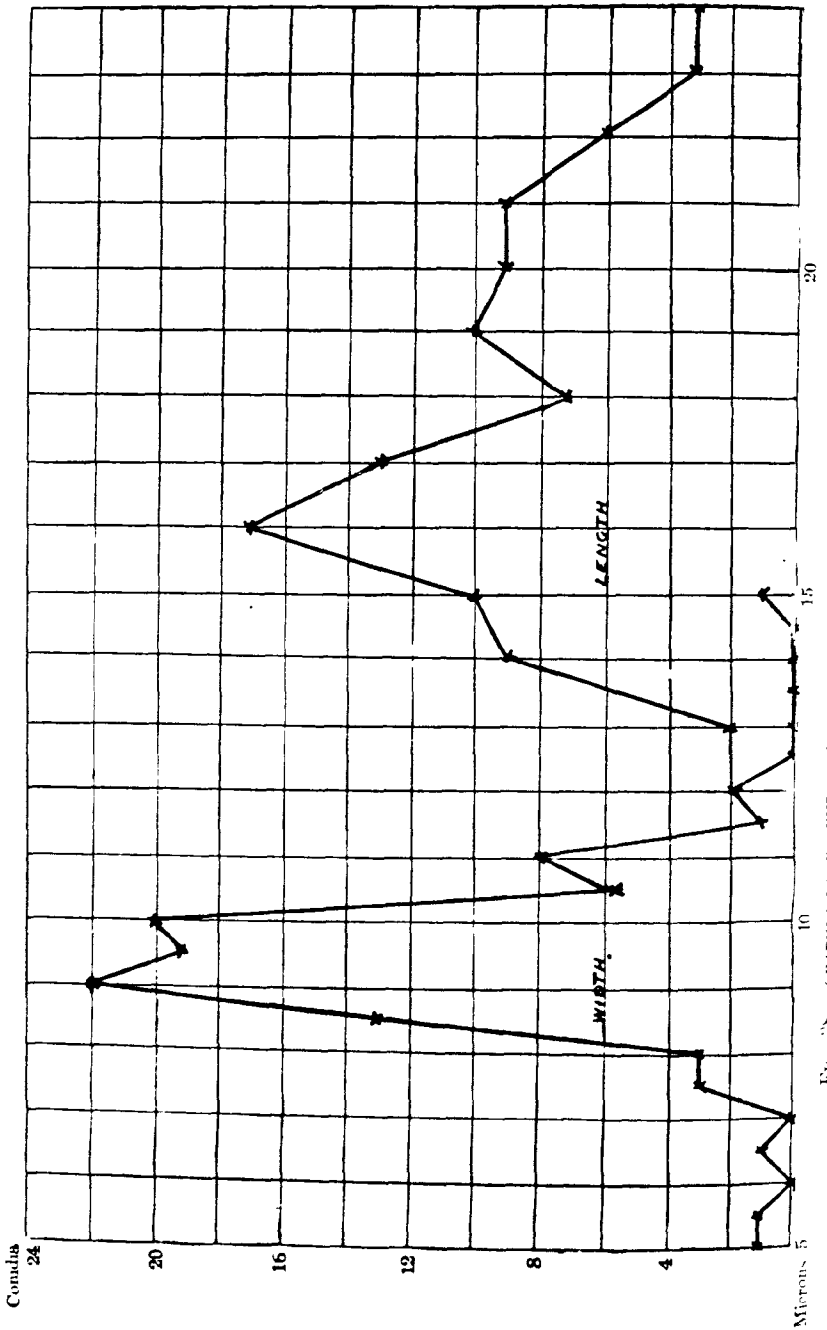


FIG. 38 GRAPHIC REPRESENTATION OF CONIDIAL MEASUREMENTS OF BOTRYTIS TULIPAE

Showing the distribution of 100 conidia. The ordinates show the number of conidia, the abcissæ, their length or width in microns

It is of little importance to describe at length the growth on other media: sucrose is utilized as a source of carbon apparently as successfully as glucose; on a glucose solution, without mineral nutrition, the growth is very poor: on plain agar and water the growth is sparse and the mycelium tends to spread; but on agar containing a mineral-nutrient solution, with

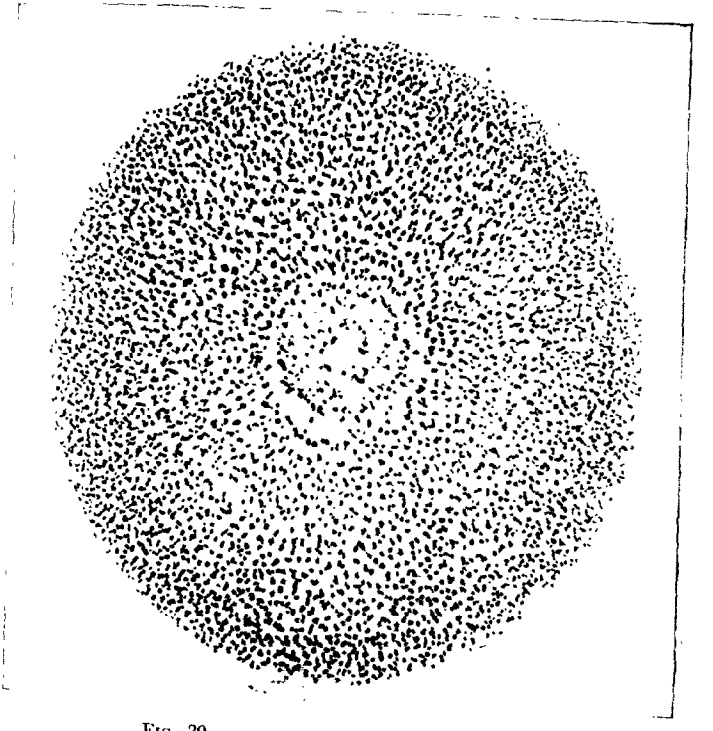


FIG. 39. SCLEROTIA OF BOTRYTIS TULIPAE
As formed in a petri-dish culture on potato agar. Natural size

no source of carbon, an excellent growth takes place, even better, perhaps, than that on potato-dextrose agar. This indicates that the carbohydrates of the agar itself are being utilized. With oxalic acid as a carbon source, the growth is poor.

Growth is best on an acid medium, and, although no experiments have been made to determine the range of acidity, good development has

always been observed when the acidity was approximately +20 according to Fuller's scale. Perhaps the range is as wide as that determined by Munn (1917:407–408) for the growth of *Botrytis Allii*.

Conidia production

Although conidia are produced abundantly in nature on tulip leaves, in agar culture under the ordinary laboratory conditions they rarely appear. The fungus tends rather to form sclerotia. However, early in 1917 the writer observed for the first time that conidia had formed under these conditions when some conidiophores developed in five petri-dish cultures. It should be noted that these conidia were produced without any special treatment, and that, although they were produced once or twice afterward, this is rather unusual under the conditions obtaining in ordinary culture vessels.

On March 17, 1917, sterilized tulip leaves in large test tubes, 20 x 2.5 centimeters in size were inoculated with cultures of three different strains in duplicate. In two of these strains a fluffy mycelium soon developed, which spread along the leaves. After about ten days conidiophores began to develop, usually toward the top of the culture, and by March 31 there was an abundant development of conidiophores close to the surface of the leaves just beyond the aerial mycelium as well as on the mycelium itself. The conidia produced were able to cause infection in healthy tulips. This experiment was repeated on April 27, 1917, and the cultures were observed daily in order to note the first appearance of the conidia. This occurred in five cultures on May 8.

Some time later, Professor Whetzel suggested that a partial drying of the plate cultures, after a good growth of mycelium had started, might produce conidia. This experiment was accordingly performed, and the partial drying was accomplished by so placing the petri-dish cover as to expose part of the agar surface, thus permitting more rapid evaporation. The petri dishes were usually left overnight in a dust-free chamber and were tightly covered again the next morning. Conidia were in this way produced successfully in a large number of instances, not only from *B. Tulipae*, but also from other Botrytis species which do not readily fruit in culture. On halves of sterilized tulip bulbs in petri dishes the fungus was also found to fruit abundantly. There seems to be a relation between conidial

production and the relative humidity over the culture, or, to state it more concisely, a relation between the rate of evaporation and conidial production.

There is, perhaps, something inherent in the nature of the host tissue which makes it an especially good substratum for the production of conidia; but it is more likely that the fungus finds in such cultures more variation in the moisture relations. This would explain why, in the experiments with sterilized tulip leaves, the conidia were not produced uniformly throughout the culture but only on a limited area toward the top of the culture tube, where the moisture relations were presumably most favorable.

Dissemination of conidia

The peculiar twisting of the conidiophores, already mentioned, is thought to have some relation to the dissemination of the conidia. In the first place, the conidia fall away very readily. This becomes obvious when an attempt is made to mount conidiophores bearing conidia in a liquid medium or if a conidiophore is jarred slightly. Secondly, the conidiophores are very hygroscopic, and a small change in the atmospheric moisture will cause them to twist with considerable violence and frequently even to dislodge the conidia. This phenomenon can be easily observed in this and in other Botrytis species by placing the specimen under a binocular microscope. Merely breathing on it gently suffices to produce these contortions. It may be concluded that in nature, owing to the frequent changes in humidity that occur, conidia are commonly dislodged in this manner and carried off by air currents.

The conidia are usually wind-borne. The writer has found that inoculations with conidia are best made by either blowing or dusting them on the host plants and subsequently spraying water on them with an atomizer.

Pathogenicity

The pathogenicity of *Botrytis Tulipae* was first demonstrated by Klebahn (1905 6), who inoculated tulip bulbs with sclerotia from a pure culture. However, he appears not to have done much exact inoculation work, and, with the exception of the experiment cited, did not use pure cultures in his infection tests. The writer does not consider that Ritzema Bos

(1903a:24) demonstrated the pathogenicity of the organism by his investigations, for he did not use pure-culture methods, but merely developed Botrytis conidia on leaves in moist chambers and then dusted the conidia on sliced bulbs, causing the bulbs thus treated to decay.

Experimental methods

The writer made isolations of the fungus from material obtained from many localities in Holland, Germany, England, Canada, and the United States. These isolations were made both from dry specimens (for it was found that the fungus would retain its vitality for a long time without moisture) and from recently infected plants. Moreover, they were made from sclerotia, mycelium, and conidia from various parts of the host—bulbs, stalks, leaves, buds, perianth, and stamens.

Although Klebahn (1905:12) found it difficult to obtain pure cultures from the sclerotia, the writer has experienced little difficulty in isolating from sclerotia by the following method: The sclerotium is rubbed free from all adhering material with a clean piece of cheesecloth, and is dipped for instant in 95-per-cent alcohol to remove the surface film of air, that is, to wet the surface. It is then placed in a 1:1000 mercuric-chloride solution for about thirty seconds, after which it is quickly removed with sterilized forceps and placed in a drop of sterilized water in a sterilized petri dish. To thoroughly remove the mercuric chloride, the sclerotium is then rinsed in several successive drops of sterilized water in the same petri dish. Usually six washings are sufficient. The sclerotium, thus prepared, is cut into four pieces and planted on a poured plate of potato-dextrose agar. The whole operation should not take more than five minutes. The writer has used this method in isolating several hundred Botrytis specimens as well as specimens of other fungi, and rarely has a contamination occurred.

Fungi may be isolated from leaf tissue in this way if care is taken not to leave the material too long in the alcohol. In these experiments the mycelium was usually isolated from the leaf tissue and the stems by cleaning the epidermis with alcohol and then peeling it back, or often, when using stems and bulbs, by breaking or splitting them open so as to expose an uncontaminated surface. Small parts of the diseased tissue were then picked out with a sterilized, sharp-pointed scalpel and planted in agar.

Conidia were isolated in several ways. Sometimes they were blown over the surface of the agar from the bent end of a platinum needle. The needle was attached to a piece of glass tubing which served as a blowpipe. The tendency at first was to gather too many spores on the needle, but with practice a sparse sowing was readily made and transfers were then obtained from the resulting colonies. Another method was to pick off, with sharp-pointed forceps, a single conidiophore, under a binocular microscope if possible, and then touch it to an agar plate in several places. Pure cultures usually resulted from some of these plantings, and often all the cultures were pure.

Pure line cultures were obtained in two ways: first, by planting the fungus on a poured plate of plain agar and water, which caused the mycelium to spread out in its growth so that a single mycelial tip could be marked under the low power, cut off, and transferred; secondly, by the isolation of a single spore. In the latter method, which was the one most frequently employed, care was necessary lest more than a single spore should be obtained. A thin layer of agar containing a few conidia was poured into a petri dish and the spores were allowed to germinate slightly. After a conidium was marked and transferred to a poured plate, a microscopical examination was always made to ascertain positively that not more than one spore had been cut out. The growth of these cultures on potato agar is characteristic and is described under *Physiology* (page 355).

Both mycelium and conidia were used as inoculum. The mycelium inoculum was prepared by growing the fungus in a petri-dish culture until the colony had reached the size of an inch or so in diameter. Small cubes of agar containing mycelium were then cut with a sterile scalpel from the edge of the colony and placed on the plant part to be inoculated, with the side containing the mycelium against the host. To prevent the inoculum from drying out, the plants were either placed in a large, moist chamber or covered with a bell glass or a lamp chimney. When it was desired to injure the inoculated parts, this was done by pricking a sterile, sharp-pointed scalpel through the agar block into the host tissue.

In using conidia, difficulty was at first experienced in attempting to spray the plants with spore suspensions in water. No infections resulted. As already mentioned, this is explained by the fact that the conidia are

not readily wet with water and consequently the water sprayed contained but few conidia in suspension. This was demonstrated by a microscopical examination of the drops on a slide sprayed with the suspension. Very few spores were found, and hence the chances for infection were slight. Since this method was unsatisfactory, an attempt was made to secure infection by dusting the conidia on with a camel's-hair brush. This proved to be very successful, and abundant infection resulted, both on dormant bulbs and on growing tulip plants. Plants inoculated in this manner were sprayed with sterile water from an atomizer and kept moist overnight.

Results of inoculations

The results obtained from inoculating dormant tulip bulbs with mycelium are shown in table 1. From this table it is clear that the dormant bulbs must be injured at the point of inoculation in order that

TABLE 1. RESULTS FROM INOCULATING DORMANT TULIP BULBS WITH MYCELIUM

Culture	Number of bulbs inoculated		Number of bulbs infected	
	Injured	Uninjured	Injured	Uninjured
B. 298 . .	4	2	4	0
B. 163. . .	2	1	2	0
B. 112. . . .	2	1	2	0
B. 149. . .	2	1	2	0
B. XVII	2	1	2	0
B. XXVII	2	1	2	0
B. XXXII	2	1	2	0
Total	16	8	16	0

* The arabic numerals represent cultures from domestic sources, and the roman numerals those of foreign origin.

mycelium may infect them. Briefly stated, the entire sixteen of the dormant bulbs which had been injured were infected by the inoculation, whereas none of the eight uninjured bulbs were thus affected. On the other hand, when ten bulbs were inoculated just after the flowers had been cut, all became infected, although only five were previously injured.

A summary of the results obtained from inoculating tulip stems with mycelium appears in table 2. From this table it is evident that the tulip stems inoculated with twelve different cultures of *Botrytis Tulipae*, five

TABLE 2. RESULTS FROM INOCULATING TULIP STEMS WITH MYCELIUM

Culture*	Number of stems inoculated		Number of stems infected	
	Injured	Uninjured	Injured	Uninjured
B. 298	3	3	3	3
B XXVII	4	5	4	3
B XXV	4	5	2	2
B. XXVI	4	5	4	5
B XVII	4	5	4	5
B. XXXII	4	5	4	5
B. 112	3	3	3	2
B. 143	3	3	3	3
B 149	3	3	3	3
B. 150	3	3	3	3
B. 163	4	5	4	5
B 414	1	2	1	1
Total	40	47	38	40

*The arabic numerals represent cultures from domestic sources, and the roman numerals, those of foreign origin

TABLE 3 RESULTS FROM INOCULATING TULIP LEAVES WITH MYCELIUM

Culture*	Number of leaves inoculated		Number of leaves infected	
	Injured	Uninjured	Injured	Uninjured
B XXVII	1	2	1	0
B. XXV	1	2	1	2
B XXVI	1	2	1	2
B. XVII	1	2	1	2
B XXXII	1	2	1	2
B 163	1	2	1	2
B 414	1	2	1	1
Total	7	14	7	11

*The arabic numerals represent cultures from domestic sources, and the roman numerals, those of foreign origin

from foreign sources and seven from domestic, showed thirty-eight infections out of forty when pricked with a needle after inoculation, and forty out of forty-seven when not injured in this way.

A summary of the results obtained from inoculating tulip leaves with mycelium is given in table 3. All seven leaves showed infections when inoculated and injured; of the uninjured leaves, eleven out of fourteen showed infections.

Tulip flowers were inoculated with mycelium, with results as given in table 4. The tulip flowers, like the leaves, were all seven infected when an injury was made at the point of inoculation. Out of fourteen not so injured after inoculation, twelve showed infections.

TABLE 4. RESULTS FROM INOCULATING TULIP FLOWERS WITH MYCELIUM

Culture*	Number of flowers inoculated		Number of flowers infected	
	Injured	Uninjured	Injured	Uninjured
B. XXVII	1	2	1	1
B. XXV	1	2	1	2
B. XXVI	1	2	1	2
B. XVII	1	2	1	2
B. XXXII	1	2	1	2
B. 163	1	2	1	2
B. 414	1	2	1	1
Total	7	14	7	12

* The arabic numerals represent cultures from domestic sources, and the roman numeral those of foreign origin

It should not be deduced that the lower proportion of infections in the uninjured leaves, stems, and flowers was owing to the inability of the fungus to penetrate uninjured tissue. The writer attributes it rather to experimental error; for the inoculum was more likely to be lost or dried out before infection had opportunity to take place than when it was placed at once in such intimate contact with the host tissue as was the case when the latter was injured.

On April 3, 1917, six dormant bulbs were dusted with conidia from a pure culture of strain B. XXVII, and by April 25 five of these were

strongly infected and some showed aerial mycelium arising from the lesions. On April 18, 1917, ten, clean, dormant bulbs were inoculated in the same manner with conidia from a culture of strain B. XXVII. In several days, nine of these showed numerous spots or streaks, varying in color from yellow to brown, where the conidia had been sown.

On March 30, 1917, at 5 p. m., four tulip leaves were dusted with conidia from a pure culture and the following morning at nine o'clock small water-soaked spots had appeared, a microscopical examination of the epidermis of which showed that the conidia had germinated and had penetrated the cuticle. On April 2 these spots showed a rusty color and were surrounded by translucent, water-soaked areas.

On April 1, 1917, at 4 p. m., three tulip plants in pots were inoculated with conidia of strain B. XXVII and placed under a large bell glass. On April 2, at 9 p. m., all had developed a considerable number of infections, as shown by the large number of small, yellow spots. These spots later become larger and of a somewhat reddish cast. About five days later the plants were severely diseased and showed a mycelial growth on the leaf surface. About seven days thereafter conidia were formed. On April 12 some sclerotia were noted in the leaf tissue.

On April 13, 1917, eight tulip plants were inoculated with conidia of strain B. XXVII and placed in a large moist chamber. On April 16 all showed numerous yellow-to-reddish spots on the leaves. A few similar spots appeared on the stems. By April 18, the small spots had coalesced and appeared as large, reddish lesions, some of which were covered with abundant conidiophores.

The inoculations with conidia are summarized in table 5. The plants were not mechanically injured at the time of inoculation.

TABLE 5. RESULTS FROM INOCULATING UNINJURED TULIP PLANTS WITH CONIDIA

Experiment	Culture	Plant part	Number inoculated	Number infected
16	B. XXVII.....	Bulb (dormant).	6	5
18	B. XXVII.....	Bulb (dormant).	10	9
14	B. XXVII.....	Leaves (detached)	4	4
15	B. XXVII.....	Tops.....	3	3
17	B. XXVII.....	Tops.....	8	8

In using mycelium as inoculum on the leaves and the stems, the lesions, after a short time, become as typical as those of the same age produced in nature. In the beginning, however, although they show the characteristic yellowing, they are not exactly like natural lesions, for they assume the shape of the agar block used in the inoculation. As the infection spreads, the region about the inoculum becomes water-soaked, then depressed, and finally dried out. At the last stage, the lesion assumes a dull gray color and produces fluffy mycelium and sometimes also a conidial layer. The lesions tend to elongate in the direction of the stem and the leaf. If an inoculation is made on the edge of a young leaf near the tip, the peculiar twisting described on page 323, under the heading *Symptoms*, results. The whole plant top may be involved as a result of such an inoculation (fig. 42). On the dormant bulbs, also, the lesions are typical (fig. 41) with a dark brown, shiny surface. In using conidia as inoculum, the lesions are typical from the start and are essentially as described on pages 319 to 328.

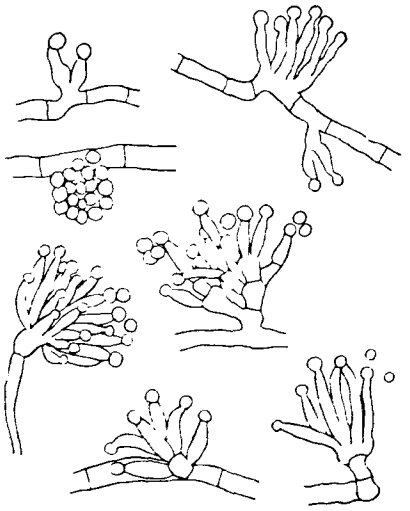


FIG. 40. MICROCONIDIA OF BOTRYTIS TULIPAE. × 600
(Camera-lucida drawing)

With but few exceptions, when infection was positive, the fungus in these experiments was re-isolated in pure culture by one of the isolation processes described under *Methods*, and checked identically with the original culture. Usually the tissue-planting method was the one employed.

In order to determine the range of parasitism of this species, a considerable number of experiments were made on both closely related and distantly related plants to find out whether *Botrytis Tulipae* is able to infect them.

The general results of these experiments appear in table 6. Certain of these, however, should be discussed more fully.

TABLE 6. RESULTS OF INOCULATION ON VARIOUS HOSTS FROM INOCULATING PLANTS NEARLY AND DISTANTLY RELATED TO THE TULIP

Plant	Inoculum	Number inoculated		Number infected	
		Injured	Uninjured	Injured	Uninjured
Lily of the valley	Mycelium..	14	0	0	
Onion (leaves)	Mycelium...	3	3	3	0
Onion (bulbs)	Mycelium..	16	1	0	0
Onion (stems)	Mycelium..	2	0	0	
Lilium sp.	Mycelium..	6	6	0	0
Narcissus (leaves)	Mycelium....	11	11	11	0
Narcissus (leaves)	Conidia	0	5		0
Narcissus (stems)	Mycelium..	3	3	3	0
Hyacinth (leaves)	Conidia.	0	5		0
Crocus (tops)	Mycelium..	7	7	7	0
Crocus (bulbs)	Mycelium.. .	5	5	5	1
Gladiolus	Mycelium..	10	0	0	
Peony	Mycelium..	19	0	3	
Potato	Mycelium..	21	0	0	
Golden seal	Mycelium..	6	0	0	

From table 6, the relation of *B. Tulipae* to certain plants is evident: it is not able to attack at all the lily of the valley, the lily, the gladiolus, the potato, or the goldenseal, and, probably, not the peony. However, this relation will be made clearer by a discussion of certain observations made during the attempts to cause infection on these plants.

Inoculation of onion.— Leaves and stalks of onion plants were inoculated with three different cultures, one of these a typical culture of *B. Tulipae*. In those plants that were injured at the time of inoculation, strong infection took place on the leaves but none occurred on the stems. On the uninjured plants there was no infection. To serve as checks, other plants were inoculated at the same time with

FIG. 41. RESULT OF ARTIFICIAL INOCULATION

Lesion on dormant bulb. The bulb was injured at the point of inoculation. Natural size

mycelium from a culture of the onion Botrytis, *B. Allii* Munn, and with a large sclerotial form of Botrytis from tulips — not *B. Tulipae*. From both of these inoculations a strong infection resulted on the leaves and a slight infection on the stem, in the uninjured as well as the injured plants. A similar experiment with mycelium from the same cultures was tried on onion bulbs, and here *B. Tulipae* produced no infection, while the other two species produced a strong infection, but only on the injured bulbs. It is interesting to note here that on the uninjured bulbs inoculated with *B. Tulipae*, peculiar depressions appeared in the bulb scale that at first seemed to be slight infections. However, microscopical examination showed that the mycelial threads had not penetrated. They were merely superficial. Nevertheless, beneath the mycelium some epidermal cells and other deeper-lying cells had been killed. Microscopical sections of the injured bulbs showed mycelium in the punctures made by the scalpel. It had not, however, penetrated laterally into the tissue, although some of this tissue had been killed.

FIG. 42. RESULT OF ARTIFICIAL INOCULATION
The whole top is involved. Natural size

Inoculation of narcissus.— The result obtained on the narcissus was similar to that on the onion: strong infections appeared on the leaves and slight ones on the stems when the inoculation was performed on

mechanically injured plants. Uninjured plants were not infected. When conidia were used to inoculate narcissus, there was no sign of resultant injury, and microscopical examination of the epidermis showed the conidia to be present but not germinated.

Inoculation of hyacinth.— Detached hyacinth leaves were inoculated with conidia from pure culture. On the fifth day after inoculation, small, yellowish, depressed spots appeared. Microscopical examination of these spots showed an abundance of germinated conidia but no penetration of the epidermis by their germ tubes. Moreover, the tissue beneath the epidermis showed no mycelium.

Inoculation of crocus.— Slight infections were caused on mechanically injured crocus leaves by mycelium of *B. Tulipae*, but no infection occurred on uninjured leaves. A large sclerotial Botrytis from tulip caused no infection in either case. Very slight infections were produced on the papery scales of crocus bulbs. On injured bulbs, all the five inoculated were infected; on uninjured bulbs, only one out of five was infected. Microscopical sections of these lesions showed mycelium ramifying through the tissue, and disintegration of the cells was observed.

Discussion of parasitism

It is evident from these pathogenicity experiments that *B. Tulipae* is practically restricted to tulips. Although under certain conditions it attacks some closely related plants, even such infection occurs, almost invariably, only when there is an injury made at the point of inoculation. Furthermore, a large number of injured plants failed to become infected. When we consider the ease with which the tulip may be infected, whether mycelium or conidia be used as inoculum and whether the host plant be injured or uninjured, these apparent exceptions only make more evident its restricted parasitism. Indeed the writer believes that in those instances in which *B. Tulipae* is reported on other hosts, if the fungus were really that species, the infection took place on an injured part of the host plant. On the other hand, the pathogene shows gradation in parasitism in its feeble attempts to invade plants other than its normal host. First, there are plants such as the crocus, on which are produced only slight infections which do not spread. Next, there are plants such as the narcissus and the onion, on which the conidia do not even germinate and infection

by mycelium can begin only at an injured place. Again, there are plants such as the hyacinth, on which the conidia will germinate and cause local injury, without actually invading the plant. Finally, there is the tulip, in the case of which infections take place easily on uninjured plants.

While this series is too incomplete to be conclusive, the tendency shown is clear, and further experiments in this direction would probably furnish additional evidence of the very limited range of the parasitism of *B. Tulipae*.

Life history

Primary inoculation and infection

The fungus survives the dormant period of the bulb as mycelium or sclerotia and is planted with it in the fall. When the bulb starts into activity in the spring, the fungus starts also and sometimes spreads throughout the entire outer scale of the bulb. If the original infection is near the apex of the bulb, the shoot also is involved in the lesion and the mycelium growing from the bulb tissue infects the leaf tissue. This condition was frequently encountered in studying the disease and is well illustrated in figure 27. Usually it is only the outer, sheathing leaf that is diseased, although sometimes the whole shoot may be affected and fail to emerge from the soil. After growing in the leaf for a time, the mycelium emerges from the dead tissue and, if favorable conditions prevail, conidiophores and conidia are produced. These are formed on the aerial mycelium and also arise directly from the mycelium in the leaf. The unspecialized hyphae and the conidiophores which arise from the leaf emerge through the stomata, and in the specimens observed, only one came from each stoma.

Secondary inoculations and infections

The conidia, produced in great abundance on these first-infected leaves, furnish abundant inoculum for secondary inoculations. Although it is not improbable that they are also transported by such other agencies as insects, spattering rain, animals, and man, the conidia are for the most part scattered to the infection courts by means of the wind.

The infection courts may be any part of the tulip plant except the roots. Conidia falling on these parts germinate very quickly under proper conditions. Experiments with conidia in tulip juice and in distilled water

produced successful germination. In the former there was a good development of germ tubes overnight, while in the latter germination took place but the development of the germ tubes was poor. This experiment was conducted at room temperature. The germ tubes penetrate directly, as discussed under the heading *Pathological histology* (page 351) and cause infection. Visible evidence of infection often appears within the short period of twenty-four hours, as was demonstrated in the pathogenicity experiments. Under conditions unfavorable for germination the conidia are able to retain their viability for some time, as the following experiment illustrates.

Tulip material abundantly covered with conidia was collected on June 12, 1917, at Ithaca, New York. It was kept under laboratory conditions and the capacity of the conidia for germination was tested on June 12, June 25, July 12, and August 2. Germination of conidia was obtained at all of these dates except the last. This shows that in a dry condition the conidia retain for several weeks their ability to germinate. The lesions caused by their infections soon enlarge and produce more conidiophores and conidia, which in turn are capable of producing more infections. That these infections are continually taking place is evident from the presence of lesions of various ages on the same leaf (fig. 25).

Conidia may be carried from badly diseased tops to the bulbs, perhaps being washed down by rain. Several specimens were collected which clearly showed this. Incipient lesions were found on both the stalks and the bulbs of such plants, showing how the inoculum works down to the bulbs. These lesions increase in size and sclerotia are produced. When the bulb becomes dormant the development of the lesion is arrested and the fungus is again ready for hibernation. There is no doubt that the sclerotia retain their vitality for a long period. In fact, isolations have been made from sclerotia which have been in a resting state for several years.

Pathological histology

The material was fixed in Flemming's, in chromo-acetic, and in Gilson's fluids, was embedded in paraffin, sectioned, and stained with both Heidenhain's iron alum-haematoxylon and Flemming's triple stain. Some difficulty was experienced in sectioning lesions on the bulbs because of the numerous, large, starch grains present. In order to study the

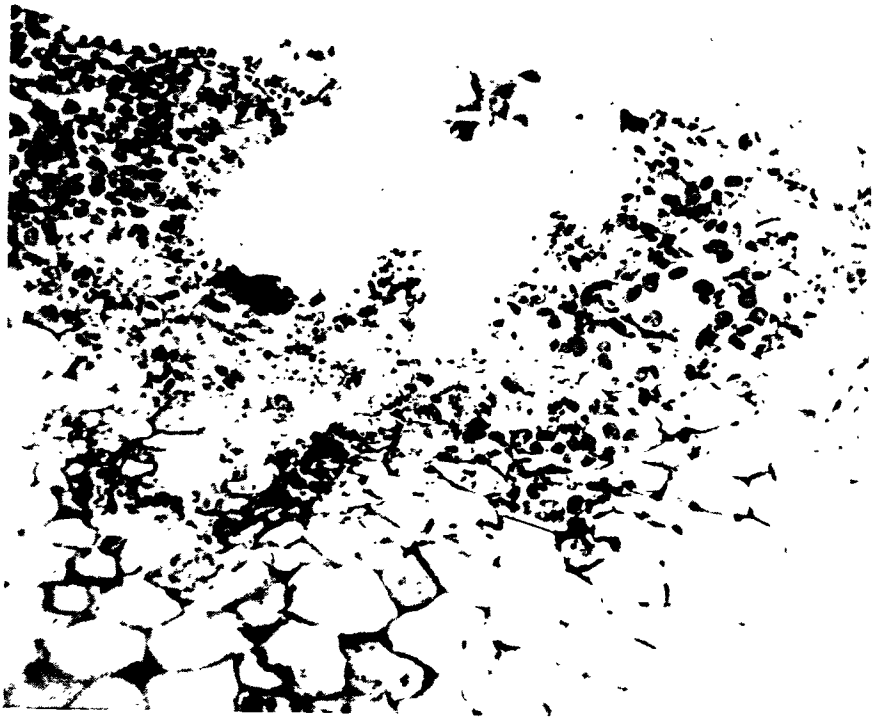


FIG. 43. LESION ON THE OUTER BULB SCALE

Photomicrograph of cross section through lesion. The accumulation of starch in the cells and an incipient sclerotium, are visible

penetration, certain areas on the tulip leaves were marked with india ink, inoculated by dusting with conidia, and, after various intervals, cut out, killed, fixed, and stained.

On the bulbs, typical necrotic lesions appear, which show a peculiar accumulation of starch about the diseased area. This is pictured in its general features in figure 43, and in more detail in figures 44 and 45, one of which shows a diseased area and the other a healthy one. These starch grains are heart-shaped and large. They react to iodine in potassium iodide in the usual way, and with Flemming's triple stain are colored a beautiful pink. Why they should accumulate in this manner about the lesion is not known.

The mycelium in the bulbous tissue is usually of small diameter and is both inter- and intracellular. Usually in that part of the tissue where the mycelium is advancing and the cells are not yet killed, it is intercellular, while in the older part of the lesion the hyphae penetrate into the cells as well as between them. The protoplasm of the cells at this stage is practically gone. The collapse of these empty cells causes the lesion to be depressed. Sclerotia sometimes form on the surface of the lesion. In figure 43 an incipient sclerotium may be seen.

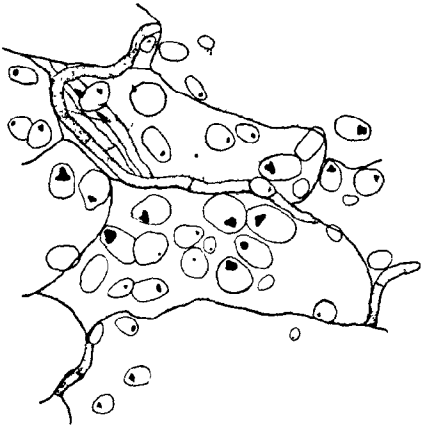


FIG. 44. STARCH ACCUMULATION IN DISEASED TISSUE. × 277

Starch cells in a diseased area of an outer bulb scale, showing numerous starch grains and intercellular mycelium. (Camera-lucida drawing)

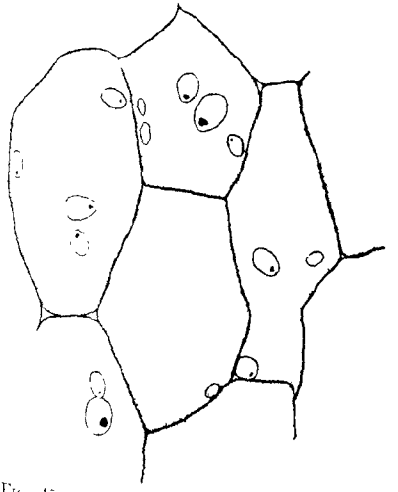


FIG. 45. HEALTHY BULB TISSUE. × 277

The amount of starch shown here may be compared with that shown in figure 44

Vascular bundles in the bulb scale were markedly affected, and in one case the xylem had entirely disappeared while the phloem, though attacked, still remained in part. In another specimen the bundle had been disintegrated on the side toward the lesion. This involved the phloem, the cells of which stained a deeper blue. There was starch accumulation in this region.

Penetration of the fungus into the leaf tissue has been observed. No appressoria are formed by the germ tubes, which instead penetrate directly through the leaf surface, either through stomata or

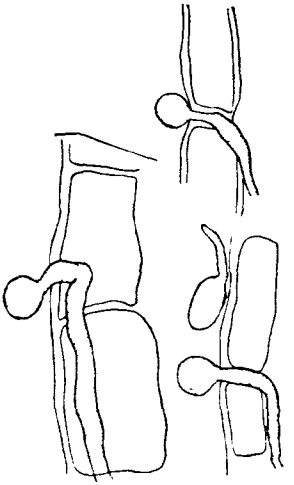


FIG. 46. PENETRATION OF LEAF TISSUE. × 277
Transverse section of epidermis. (Camera-lucida drawing)

between epidermal cells (figs. 46, 47). The germ tubes have not been observed to penetrate directly through epidermal cells. It has been noted that penetration more often occurs where the conidia are more numerous. Probably this is because of the greater enzymatic action, which hydrolyzes the cuticular substance.

The mycelium in the leaf, like that in the bulb, is both inter- and intracellular. This is shown in figures 48 and 49. After the fungus has developed for a time in the leaf tissue, a collapse of the cells results and causes the leaf to become much thinner in the diseased area. Here also, where the mycelium is still intercellular, the cells are not killed. There is injury caused in advance of the mycelium. This indicates the excretion of toxic or enzymatic substances by the pathogene.

The writer thinks that the injury caused in this disease is not due to oxalic acid. Some experiments were made to determine what the nature of the injury from oxalic acid would be. Several plants were injected hypodermically with solutions of oxalic acid of various concentrations, and lesions were produced which strikingly resembled those caused by a fungus. Furthermore, microscopical examination indicated that no fungus had been accidentally introduced. However, the concentrations were necessarily higher than those produced by fungi in culture. The work of Brown (1915) seems to show that neither oxalates nor oxalic acid take part in the toxicity of *B. cinerea*, but

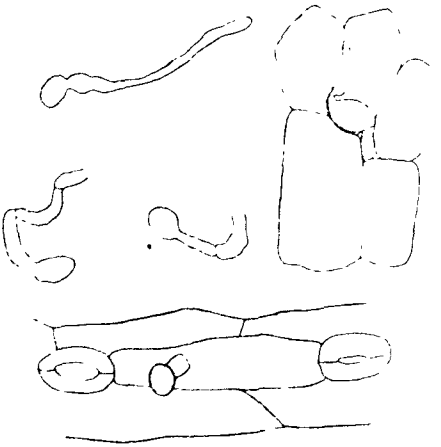


FIG. 47. PENETRATION OF LEAF TISSUE. × 277
Surface view. (Camera-lucida drawing)

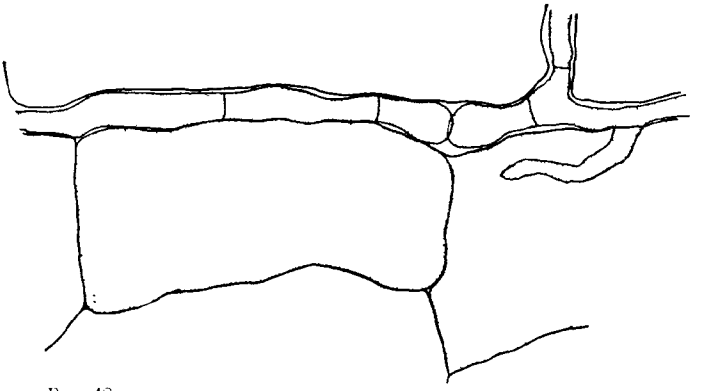


FIG. 48. INTERCELLULAR MYCELIUM IN LEAF TISSUE. × 600
The cells have not yet lost their protoplasm. (Camera-lucida drawing)

that this toxicity is due to enzymatic action.

CONTROL

It has been impossible to carry control experiments far enough to justify making any definite recommendations for the control of *Botrytis Tulipae*. A consideration of the pathogene, however, makes it evident that elimination is probably of first importance. Clean bulbs, free from mycelium and sclerotia, should produce clean tulips, for it is most probable that in these forms the pathogene is carried on the bulbs. Although the disease may possibly be attributed to infested soil, it often occurs on tulips grown in soil in which heretofore no tulips have been grown.

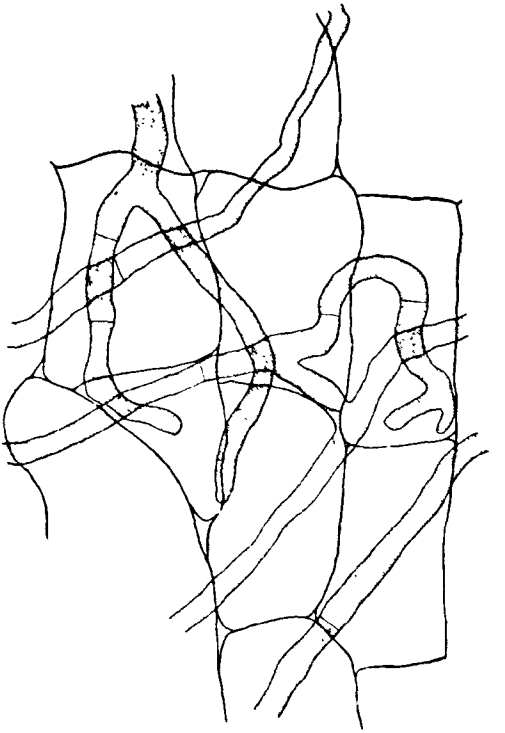


FIG. 49. INTRACELLULAR MYCELIUM IN LEAF TISSUE. × 600
The cells of the leaf are devoid of contents. (Camera-lucida drawing)

FIG. 50. PROLIFERATION OF CONIDIOPHORE. × 840
Showing new branches arising from conidial cluster. (Photomicrograph)

Until further experiments have been made, soil treatment cannot be recommended. Carbolineum has been recommended in the literature as a disinfectant for soil (Elenkin, 1911). Klebahn (1904:33) criticizes this method unfavorably, saying that not even weeds will grow in soil thus treated.

Experiments made at Madison, Wisconsin, in 1917, showed that spraying tulips with bordeaux mixture 5–5–50 caused considerable injury to both the leaves and the flowers, besides giving them an unsightly appearance. Accordingly this treatment is not to be recommended.

From the present knowledge of this disease the following measures seem advisable:

1. Selection of clean bulbs, free from lesions and sclerotia. When the sclerotia occur only on the outer papery scale this should be removed and burned. It is well also to inspect the old stalk of the previous year, if this still remains attached, for it frequently bears sclerotia (fig. 22).

2. Careful handling, to avoid injuring the bulbs, as infection takes place more readily on injured bulbs than on healthy ones.

3. Storage of the bulbs under proper conditions of temperature and humidity. The temperature should be kept as low as possible without injury to the bulbs, preferably about 40° F. The humidity also should be low. These conditions are especially desirable, as they retard the development of any small lesions that may be present on the bulbs at the time of storage, and prevent the germination of any conidia that may be on their surface.

4. Removal and destruction of diseased plants when they appear in the field or the beds. This will limit, if it does not entirely prevent, secondary infections.

SUMMARY

An investigation of the tulip disease caused by *Botrytis Tulipae* (Libert) comb. nov. shows that it is present throughout the United States and that it was probably introduced with the introduction of tulip bulbs. Reports of the disease show that it has been in this country at least since 1901.

Under normal conditions this disease is restricted to the genus Tulipa and within this genus practically all varieties are susceptible. One instance of apparent immunity is the variety Baronne de la Tonnaye, which, during an epidemic of Botrytis blight, showed no evidence of the disease.

Counts made in the spring of 1917, at Ithaca, on one variety of late tulips, Spathulata, showed 100 per cent of the leaves and 98 per cent of the stalks to be affected. Other varieties were similarly infected. These infections were traced to the bulbs, of which the variety Spathulata showed 4.6 per cent with unmistakable Botrytis lesions and the Mrs. Grover Cleveland variety, 5.2 per cent.

The disease is easily recognized on the bulbs when the fungous sclerotia are present in the lesions. On the leaves, the flower stalks, and the flowers, a severe blighting frequently takes place.

Studies of the literature and herbarium specimens show that the disease under consideration is to be ascribed to *Botrytis Tulipae* (Libert) comb. nov.[4]

Cultural studies have demonstrated that both the small sclerotia on the bulbs and the conidial form on the leaves and other parts of the tulip plant are stages of one and the same fungus, namely, *Botrytis Tulipae*.

[4] In recent literature the fungus has gone by the name *Botrytis parasitica* Cavara, but the specific name of Libert has priority.

The morphology of the parasite has been investigated in some detail. The manner of formation and attachment of the conidia has been brought out, microconidia have been demonstrated for this species and conidial measurements show that while the variation in size is from 12–24 x 10–20, the greater number of spores measure 16–17 x 9–10.

Conidial production, which rarely takes place in pure cultures under ordinary conditions, was found to occur abundantly when plate cultures were partially dried. Abundant conidia were also formed on sterilized tulip leaves in large test tubes.

The parasitism of *B. Tulipae* has been fully demonstrated by numerous infections brought about by the use of pure cultures of the organism. Inoculations of other plants, both nearly and distantly related, while showing the parasite to be restricted to tulips, show also that the parasite exhibits a weak and varying degree of ability to attack other plants.

Hibernation is by means of sclerotia which live over the winter on the bulbs. Infection spreads from these bulbs to the developing shoots, where abundant conidia are produced. These primary lesions serve as the source of inoculum for secondary infection. The conidia produced in this manner retain their vitality for several weeks.

Sections through lesions on the bulb show an accumulation of starch about the diseased area. In the penetration of the tissue by conidial germ tubes, no appressoria are formed and the germ tubes penetrate directly through the epidermis or through the stomata.

Although extensive control experiments have not been made, it is recommended that clean bulbs, careful handling of bulbs, proper storage, and systematic removal and destruction of diseased plants in the field will largely hold the disease in check.

Memoir 39, *The Genetic Relations of Plant Colors in Maize*, the sixth preceding number in this series of publications, was mailed on July 19, 1921

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EPTEMBER, 1921 MEMOIR 46

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

A CLASSIFICATION OF THE CULTIVATED VARIETIES OF BARLEY

ROY GLEN WIGGANS

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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A CLASSIFICATION OF THE CULTIVATED VARIETIES OF BARLEY

A CLASSIFICATION OF THE CULTIVATED VARIETIES OF BARLEY

ROY GLEN WIGGANS

The need for systematic classifications of the various farm crops has been recognized in recent years, due to the large increase in the number of varieties and the confusion in the nomenclature. It is the purpose of this study to make a classification of barleys that will aid agronomists, seedsmen, and farmers to identify the different varieties in common cultivation and to clear up the misuses of nomenclature.

Before a classification of any group of plants can be undertaken, it is necessary to have an accurate knowledge of the structure of the plants. For this reason, and because it is hoped that the descriptions may be of value to detailed studies in the future, the morphology of the barley plant is fully discussed in this paper.

WORK OF OTHER INVESTIGATORS

CLASSIFICATIONS

The numerous and extensive researches on barley already available have been made largely in Europe, and deal more with the malting and brewing qualities of the barley grown and the processes of manufacturing than with systematic classification. This work, however, has not been entirely neglected. Classifications have been presented by various European and American investigators. On close examination, these classifications are found to differ widely in arrangement and in the weight given the various characters that have been used in distinguishing between the species and also between groups of lesser importance. For these reasons, and in order (1) to make available the classifications of European investigators and (2) to give weight to the characters employed in the present classification, considerable space is devoted in this paper to reviewing the various classifications that have previously been presented.

The earliest classification of barleys of any importance was that of Linnaeus (1718)[1]. Five years later (1753) he elaborated on his first work,

[1] Dates in parenthesis refer to *Bibliography*, page 449.

recognizing four distinct species and two varieties of cultivated barleys, as given briefly in the following key:

A. All spikelets fertile.
  B. Spikes dense ..... *Hordeum hexastichon* L.
  BB. Spikes lax ..... *H. vulgare* L.
    C. Kernels hulless ..... *H. vulgare var. coeleste* L.
AA. Median spikelet fertile.
  B. Spikes dense ..... *H. zeocriton* L.
  BB. Spikes lax ..... *H. distichon* L.
    C. Kernels hulless ..... *H. distichon var. nudum* L.

In making his classification Linnaeus recognized three important taxonomic characters — fertility, density, and adherence of lemma and palea to the caryopsis. These three characters have been given important consideration in practically every classification made since, and the species established by Linnaeus have been the foundation of all subsequent work. All classifications previous to that of Linnaeus were necessarily based on very small collections, and as a consequence only two types of barley, the six-rowed and the two-rowed, were recognized. For this reason, nothing is to be gained by a review of the literature previous to 1753.

No work was done on barleys for sixty-five years after the publication of Linnaeus' classification. Schübler (1818) named seven species by employing the same characters as were used by Linnaeus. The only addition he made was the separation for the first time of the Linnaean species *distichon* into *erectum* and *nutans*. This separation was made on density, thus giving three species of two-rowed barleys, *zeocriton*, *erectum*, and *nutans*, based on the density of the spike.

Following Schübler, Séringe (1819) recognized four species, all of which had been named by Linnaeus. Later (1841–42) he made subdivisions of the four species but failed to add anything of value to previous work.

Jessen (1855) presented a brief classification wherein he considered all cultivated varieties of barley as one species, namely, *Hordeum sativum* Jess. He was the first botanist to thus limit the number of species of cultivated barleys.

Heuze (1872), working with a much larger collection of barleys than his predecessors used, was able to expand and enlarge on the classifications previously presented. His work doubtless stimulated later workers, especially Körnicke, who published *Die Saatgerste* (1882) and later elaborated on this work in the *Handbuch des Getreidebaues* (Körnicke, 1885).

The classification of Körnicke, as presented in 1885, is given briefly in the following key.[2] He considered all cultivated varieties to belong to one species, *Hordeum vulgare* L., and established four primary groups within the one species, using fertility, terminal appendage, and number of rows or ranks as the chief characters.

A. All spikelets fertile . . . . . *Hordeum polystichum* Doll.
B. All spikelets awned.
C. Six-rowed barley, the spikes with six similar rows . . . *H. hexastichum* L.
CC. Four-rowed barley, the spikes with four dissimilar rows; two opposite rows formed by the overlapping of two spikelets. . . . *H. tetrastichum* Keke.
BB. Only the middle spikelets awned, middle barley . . . *H. intermedium* Keke.
AA. Only the middle spikelets fertile. Two-rowed barley . . . *H. distichum* L.

The varieties within the four subspecies which Körnicke established are as follows:

I. *Hordeum hexastichum* L.
A. Kernels hulled.
B. Outer glumes normal, linear.
C. Spike yellow.
D. Grain short . . . . . var. *brachyatherum* Keke.
DD. Grains long.
E. Spike pyramidal . . . . . var. *pyramidatum* Keke.
EE. Spike with parallel sides . . . . . var. *parallelum* Keke.
CC. Spike black.
D. Spike short, somewhat pyramidal . . . var. *Schimperianum* Keke.
DD. Spike long, with parallel sides . . . var. *gracilius* Keke.
BB. Outer glumes all or in part broadly lanceolate.
C. All outer glumes broadly lanceolate . . . var. *curtipes* Keke.
CC. Only the outer glumes of the lateral spikelets broadly lanceolate. var. *recens* Keke.
AA. Kernels naked. . . . . var. *revelatum* Keke.

II. *Hordeum tetrastichum* Keke.
A. Kernels hulled.
B. Glumes normal.
C. Spike yellow.
D. Grain straight . . . . . var. *pallidum* Ser.
DD. Grain twisted . . . . . var. *Heuzei* Keke.
CC. Spike gray-blue . . . . . var. *coeruleseens* Ser.
CCC. Spike black.
D. Grain rough . . . . . var. *nigrum* Willd.
DD. Grain smooth . . . . . var. *leiorrhynchum* Keke.
BB. Glumes monstrous.
C. Grain long, strong . . . . . var. *tortile* Robert.
CC. Grain short, intermediate . . . . . var. *cucullatum* Keke.
CCC. Grain weak . . . . . var. *Horsfordianum* Wittm.

[2] Translated from the original German, but is rearranged in the standard form.

AA. Kernels naked.
B. Glumes normal.
C. Spike yellow.
D. Spike long, narrow; kernel thin ..... var. *coeleste* L.
DD. Spike short; kernel thick.
E. Kernel blue-gray ..... var. *himalayense* Rittg.
EE. Kernel yellowish blue, thinner ..... var. *Walpersii* Keke.
CC. Spike gray-violet ..... var. *violaceum* Keke.
BB. Glumes monstrous.
C. Only on middle spikelet ..... var. *cornutum* Schrader
CC. On all spikelets.
D. Awned ..... var. *pseudotrifurcatum* Langsd.
DD. Awnless ..... var. *trifurcatum* Schl.

3. *Hordeum intermedium* Keke.
A. Spike thick, straight ..... var. *transiens* Keke.
AA. Spike weak, nodding ..... var. *Haxtoni* Keke.

4. *Hordeum distichum* L.
A. Rhachis at maturity remaining entire.
B. Spike normal.
C. Kernels hulled.
D. Spike with parallel sides.
E. Spike weak, narrow.
F. Spike yellow.
G. Grain rough ..... var. *nutans* Schubl.
GG. Grain smooth ..... var. *medicum* Keke.
FF. Spike blackish ..... var. *nigrescens* Keke.
FFF. Spike black.
G. Grain rough ..... var. *nigricans* Sér.
GG. Grain smooth ..... var. *persicum* Keke.
EE. Spike thick, short.
F. Yellow ..... var. *erectum* Schubl.
FF. Black ..... var. *contractum* Keke.
DD. Spike becoming smaller at point.
E. Yellow ..... var. *zeocrithum* L.
EE. Black ..... var. *melanocrithum* Keke.
CC. Kernels naked ..... var. *nudum* L.
BB. Spike abnormal.
C. Spike simple.
D. Flowers of side spikelets normal.
E. Outer glumes of middle spikelet normal ..... var. *heterolepis* Keke.
EE. Outer glumes of middle spikelet short lanceolate ..... var. *Braunii* Keke.
DD. Flowers of side spikelets entirely degenerated.
E. Outer glumes of middle spikelet short lanceolate.
F. Yellow ..... var. *abyssinicum* Sér.
FF. Black ..... var. *macrolepis* A. Br.
EE. Outer glumes of middle spikelet normal.
F. Yellow ..... var. *decrescens* Steud.
FF. Brown ..... var. *Strangii* Keke.
FFF. Black ..... var. *Steudelii* Keke.
CC. Spike branched.
D. Side spikelets normal ..... var. *compositum* Keke.
DD. Side spikelets not normal ..... var. *ramosum* Hochst.
AA. Rhachis at maturity falling apart ..... var. *spontaneum* C. Koch

Under the preceding classification Körnicke brought together and described in detail 103 sorts which varied widely in structure and also in adaptation. Some of the varieties given in the classification were not represented in his collection, while others were represented by many sorts or subvarieties. Since its publication the grouping given by this author has been considered the best one on the subject of barley varieties. In general the treatment given is very satisfactory and has been sufficient in most cases to establish varieties on a firm basis. The most apparent weakness in the scheme is in the treatment of the main groups, where a division of the six-rowed form is made on the arrangement of the rows of spikelets. The characters given the most weight by this author in the subdivisions are: adherence of the lemma and the palea to the caryopsis, shape of the outer glume, color of the grain, shape of the grain, shape of the spike, roughness or smoothness of the grain, and character of the rhachis. Two later papers by Körnicke (1895 and 1909, the latter published posthumously by his son, M. Körnicke) appeared, neither of which added anything of value to the previous paper; in fact, they lacked the clearness that was evident in the earlier publication.

Voss (1885), in the same year as that in which the *Handbuch des Getreidebaues* appeared, also published a classification of barleys. Voss considered all cultivated varieties as one species, and followed Jessen (1855) in using *Hordeum sativum* as the species name. The subspecies, varieties, and subvarieties used by Voss are as follows: [3]

A. All flowers perfect and fertile ..... subspecies *polystichon* Döll.
1. Six-rowed barleys ..... var. *hexastichon* L.
a. Spikes white ..... subvar. *album*
b. Spikes black ..... subvar. *nigrum*
2. Parallel barleys ..... var. *parallelum* Kcke.
a. Spikes white ..... subvar. *album*
b. Spikes black ..... subvar. *nigrum*
3. Unequal or odd-rowed barleys ..... var. *inaequale* Voss
a. Spikes white ..... subvar. *album*
b. Spikes black ..... subvar. *nigrum*
4. Hull-less barleys ..... var. *coeleste* L.
a. Erect barleys ..... subvar. *erectum* Voss
b. Lax barleys ..... subvar. *flaccidum* Voss
c. Hooded barleys ..... subvar. *trifurcatum* Sér.

AA. Only the middle flowers fertile, side flowers staminate; two-rowed barleys. subspecies *distichon* L.
5. Peacock barleys ..... var. *zeocrithon* L.
a. Spikes white ..... subvar. *album*
b. Spikes black ..... subvar. *nigrum*

[3] Translated from the original German.

6. Erect barleys ..... var. *erectum* Schübler
   a. Spikes white ..... subvar. *album*
   b. Spikes black ..... subvar *nigrum*
7. Nodding two-rowed barleys ..... var. *nutans* Schübler
   a. Spikes white ..... subvar. *album*
   b. Spikes black ..... subvar. *nigrum*
8. Naked two-rowed barleys ..... var. *nudum* L.

AAA. Only the middle flowers fertile, side flowers entirely lost or stunted; deficient barleys. subspecies *deficiens* Steud.

9. Dense deficient barleys ..... var. *densum* Voss
   a. Spikes white ..... subvar. *album*
   b. Spikes black ..... subvar. *nigrum*
10. Loose deficient barleys ..... var. *laxum* Voss
   a. Spikes white ..... subvar. *album*
   b. Spikes black ..... subvar *nigrum*
11. Wide deficient barleys ..... var. *platynepis* Voss
   a. Spikes white ..... subvar. *album*
   b. Spikes black ..... subvar. *nigrum*
12. Long deficient barleys ..... var. *macrolepis* A. Br.
   a. Spikes white ..... subvar. *album*
   b. Spikes black ..... subvar. *nigrum*

In the separation of his main groups Voss used only one character, that of fertility, of which he recognizes three degrees. This is a decided advance over the group separation given by Körnicke, although the treatment of varieties by Voss is much inferior to that of Körnicke. In making varietal differences, Voss uses the following characters: shape of spike, arrangement of rows of spikelets, and color.

Atterberg, working from 1889 to 1899, published several papers on barley classification, but it was not until 1899 that he presented anything differing materially from the work of previous investigators. In 1899 he published his *Die Varietäten und Formen der Gerste*, wherein he departed radically from the established systems. In designating 188 forms he used only 33 different terms. He followed Jessen in placing all cultivated varieties in one species, *Hordeum sativum*. His scheme is as follows:[1]

Subspecies (Unterarten) of *Hordeum sativum*

A. Middle spikelets awned.
   B. Glumes small ..... *Hordeum sativum commune*
   BB. Glumes large, about the length of the ripe grain, awns not considered ..... *H. sat. macrolepis*

AA. Middle spikelets awnless or hooded.
   B. Middle spikelets hooded ..... *H. sat. furcatum*
   BB. Middle spikelets awnless ..... *H. sat. inerme*

[1] Translated from the original German, but rearranged in the standard form for keys

Each subspecies was divided into the following groups (Abarten):

A. Glumes remaining attached to caryopsis at maturity.
  B. Grains light-colored . . . . . *album*
  BB. Grains dark-colored . . . . . *nigrum*
AA. Glumes lost from caryopsis at maturity.
  B. Grains light-colored . . . . . *nudum*
  BB. Grains dark-colored . . . . . *nigronudum*

Each group was then divided into the following varieties:

A. All six spikelets fertile.
  B. Side spikelets awned . . . . . *polystichum*
  BB. Side spikelets not awned; established by crossing six-rowed and two-rowed forms. *muticum*
AA. Side spikelets infertile.
  B. Glumes small, short, linear . . . . . *distichum*
  BB. Side spikelets rudimentary; outer glumes lacking or almost lacking; only small lemmas present . . . . . *deficiens*

The varieties of six-rowed barleys were each further divided into the following subvarieties:

A. Average length of rhachis internode, 1.7–2.1 mm. Spike very dense . . . *hexastichum*
AA. Average length of rhachis internode, 2.1–2.8 mm. Spike average density . *parallelum*
AAA. Average length of rhachis internode, 2.7–4.0 mm. Spike loosely formed . . *vulgare*

The varieties of two-rowed barleys were each further divided into the following subvarieties:

A. Average length of internode, 1.7–2.1 mm. Spikes very thick . . . . . *zeocrithum*
AA. Average length of internode, 2.1–2.8 mm. Spikes usually standing upright *erectum*
AAA. Average length of internode, 2.8–4.0 mm. Spikes loose, generally nodding at maturity. *nutans*

In the formation of his four subspecies, Atterberg used both the terminal appendage and the character of the outer glumes. Further divisions were made on color, adherence of lemma to caryopsis, fertility, shape of outer glumes, length of internodes, and density of spike. To make lesser groups than those given above, he used the character of the base of the kernel, the basal bristle, rough and smooth awns, and color.

This scheme of classification shows a familiarity with a wider range of types than does the work of any previous investigator. Atterberg could not have followed the systematic arrangement had he not possessed a collection in which the lesser factors constantly reappeared in important groups. The objection to the system is that confusion is bound to occur (1) in the division of the subspecies and (2) in the repetition of the same terms in all the subdivisions, even though there are only 33 terms used.

Atterberg considers the designation of 188 varieties by only 33 different terms as a decided improvement over previous classifications, but this seems to be a doubtful advantage.

In connection with the work of Atterberg, the Swedish, or Svalof, system of classification should be considered. Atterberg himself in 1889 laid the foundation for this system of classification. His work was subsequently improved upon by Neergaard (1889), but it remained for Bolin (1893) to perfect the system and put it into practice. The system which Bolin worked out at that time has been used in Sweden ever since for the identification of the important varieties. Briefly the system is as follows:[5]

A. Two-rowed barley; all kernels broadest in the middle and symmetrical in contour.
  B. Dorsal side of base of kernel with a slight horseshoe-like excavation or depression *Hordeum distichum nutans*
    C. Rhachillae and lodicules long-haired.
      D. Lateral nerves without teeth . . . . *Type I*
      DD. Lateral nerves with teeth . . . . . *Type II*
    CC. Rhachillae and lodicules short-haired, more or less woolly.
      D. Lateral nerves without teeth . . . *Type III*
      DD. Lateral nerves with teeth . . . . *Type IV*
  BB. Dorsal side of base of kernel not excavated but often pinched with a transverse crease or furrow . . . . *H. distichum erectum*
    C. Rhachillae and lodicules long-haired.
      D. Dorsal nerves without teeth . . . . *Type V*
      DD. Dorsal nerves with teeth . . . . . *Type VI*
    CC. Rhachillae and lodicules short-haired, more or less woolly.
      D. Dorsal nerves without teeth . . . . *Type VII*
      DD. Dorsal nerves with teeth . . . . *Type VIII*
AA. Six-rowed barley; all kernels from outer rows of head slightly twisted, kernels from middle rows symmetrical but broadest nearer the tip, the basal half being somewhat elongated . . . . *H. tetrastichum pallidum*
  B. Rhachillae and lodicules long-haired.
    C. Lateral nerves without teeth . . . . *Type IX*
    CC. Lateral nerves with teeth . . . . *Type X*
  BB. Rhachillae and lodicules short-haired, more or less woolly.
    C. Lateral nerves without teeth . . . . *Type XI*
    CC. Lateral nerves with teeth . . . . . *Type XII*

The great additions made by the investigations of these men were the discoveries of the stable characters of the rhachilla, or basal bristle, and the lateral nerves. These two discoveries marked a real advance in the matter of barley classification. Many other studies were made on minor differences in varieties, which were not found to be constant.

Some years later (1906) Broili published a classification of two-rowed barleys in which he used the Svalöf system to a very large extent, adding

[5] Rearranged in the standard form for keys.

little to the previous work. He, however, criticized the Svalöf investigators in regard to the constancy of the characters of the rhachilla and the dorsal nerves. This criticism has been shown by subsequent investigators to be without foundation.

Beaven (1902) presented the first comprehensive classification of barleys in English. The main groups which he considered under the one species, *Hordeum sativum*, are as follows:

A. All spikelets fertile.
  B. All spikelets normal.
    C. Spike wide with short internodes . . . . . *Hordeum hexastichum* L.
    CC. Spike narrow with long internodes . . . *H. vulgare* L; *H. tetrastichum* Keke.
  BB. Spikelets of median rows normal, spikelets of four lateral rows diminutive and without awns . . . . . *H. intermedium* Keke.
    C. Spike wide, with short internodes . . . . . .var. *Haxtoni*
    CC. Spike narrow, with long internodes . . . . . .var. *transiens*
AA. Only the median spikelets fertile.
  B. Four lateral rows infertile or staminate.
    C. Spike wide, with short internodes . . . *H. zeocriton* L.
    CC. Spike narrow, with long internodes . . *H. distichum* L.
  BB. Four lateral rows rudimentary and without floral organs (several Abyssinian varieties) . . . . . *H. decipiens* Steudel

In his main divisions Beaven used these characters: fertility and width of spike, and length of rhachis internode. He used the name *H. vulgare* L. for *H. tetrastichum* Keke., and divided the two-rowed barleys into *zeocriton* L. and *distichum* L. to correspond with the two forms of six-rowed barleys. He did not make a division of the *decipiens* group. In his description of varieties he used character of the spike (normal or abnormal), shape of the spike, color of the grain, terminal appendage, and character of the awn. His varietal descriptions include many recently developed varieties, especially those of Karl Hansen, which in several cases were not yet well established.

Regel (1906, 1908, 1910) differed from earlier workers (1) by basing his minor groups on races varying somewhat in environmental adaptations, (2) by recognizing only two densities, (3) by considering blue and purple as forms of white varieties, and (4) by making smooth awns a very minor character.

Harlan (1914) made a study of barleys somewhat paralleling that of the Svalof investigators. He made no classification, but gave the characters that are of taxonomic value a thorough study. He was able to verify the findings of many previous investigators as to the value of certain

characters in classification as well as in genetic studies. Probably the most important addition to the knowledge of barleys which he gave was that in regard to pigmentation, which is reviewed later, in the discussion of the morphology of the barley plant.

The grouping suggested by Carleton (1916) is as follows:

Hordeum
- spontaneum, K. Koch, distichum, Linn., two-row barley.
- polystichum, Döll
  - vulgare, Linn., common or nodding six-row barley.
  - hexastichum, Linn., club or erect six-row barley.
- intermedium, Keke., hybrid barley.

Carleton mentions one other type, *Hordeum distichum deficiens*, of which there are two forms, but he does not consider it as one of the main groups. Under each of the above groups Carleton separated varieties by the use of the following characters: fertility, color of the grain, shape of the spike, character of the awns, and habit of early growth. He gives only a brief consideration to the general classification, and contributes little to previous works.

A little later (1918) Harlan presented a classification which is to be commended in many respects. This is given here in detail:

Key to the species

All spikelets fertile (6-row barley).
- Lemmas of all florets awned or hooded . . . . . *vulgare* L.
- Lemmas of lateral florets bearing neither awns nor hoods . . . . . *intermedium* Keke.

Only the central spikelets fertile (2-rowed barley).
- Lateral spikelets consisting of outer glumes, lemma, palet, rachilla, and usually rudiments of the sexual organs *distichon* L.
- Lateral spikelets reduced, usually to only the outer glumes and rachilla, rarely more than one flowering glume present, and never rudiments of sexual organs. . . . . *deficiens* Steud.

This scheme is founded on the one character fertility, that of density being eliminated entirely. It likewise considers barley as consisting of four distinct species, on the grounds (1) that clearness is better secured by making the species a smaller unit, (2) that no group of wild plants of such wide variation is united under a single species, and (3) that there is abundant evidence that at least two parents were involved in the production of the forms now domesticated. The only difficulty in separating the main groups comes in a few cases in which the variety is more or less intermediate in character. As Harlan has pointed out,

his condition arises very seldom in the existing varieties. It may, owever, cause difficulty in the future as the number of varieties increases. By the use of the adherence of the lemma and the palea to the caryopsis, he terminal appendage of the flowering glume, and the color of the grain, Harlan has described eight varieties in each of his species as follows:

Key to the varieties

Hordeum vulgare.
Kernels hulled.
Lemmas awned.
Kernels white, blue, or purple. . . . . 1. *pallidum.*
Kernels black. . . . . 2. *nigrum.*
Lemmas hooded.
Kernels white, blue, or purple. . . . . 3. *horsfordianum.*
Kernels black . . . . . 4. *atrum.*
Kernels naked
Lemmas awned
Kernels white, blue, or purple. . . . . 5. *coeleste.*
Kernels black . . . . . 6. *duplinigrum.*
Lemmas hooded.
Kernels white, blue, or purple . . . . . 7. *trifurcatum.*
Kernels black . . . . . 8. *aethiops.*
Hordeum intermedium.
Kernels hulled.
Lemma of central floret awned or awnless.
Kernels white, blue, or purple . . . . . 9. *haxtoni.*
Kernels black . . . . . 10. *mortoni.*
Lemma of central floret hooded.
Kernels white, blue, or purple. . . . . 11. *subcornutum.*
Kernels black . . . . . 12. *atricornutum.*
Kernels naked
Lemma of central floret awned or awnless.
Kernels white, blue, or purple. . . . . 13. *nudihaxtoni.*
Kernels black . . . . . 14. *nudimortoni.*
Lemma of central floret hooded.
Kernels white, blue, or purple. . . . . 15. *cornutum.*
Kernels black . . . . . 16. *subaethiops.*
Hordeum distichon.
Kernels hulled
Lemmas awned or awnless.
Kernels white, blue, or purple . . . . . 17. *palmella.*
Kernels black . . . . . 18. *nigricans.*
Lemmas hooded.
Kernels white, blue, or purple. . . . . 19. *angustispicatum.*
Kernels black . . . . . 20. *rimpaui.*
Kernels naked
Lemmas awned or awnless.
Kernels white, blue, or purple. . . . . 21. *nudum.*
Kernels black . . . . . 22. *nigrinudum.*
Lemmas hooded
Kernels white, blue, or purple. . . . . 23. *laxum.*
Kernels black . . . . . 24. *nigrilaxum.*

Hordeum deficiens.
Kernels hulled.
Lemmas awned or awnless.
Kernels white, blue, or purple. . . . . 25. *deficiens.*
Kernels black . . . . . 26. *steudelii.*
Lemmas hooded.
Kernels white, blue, or purple. . . . . 27. *tricenos.*
Kernels black. . . . . 28. *tridax*
Kernels naked.
Lemmas awned or awnless.
Kernels white, blue, or purple. . . . . 29. *nudideficiens*
Kernels black . . . . . 30. *decorticatum.*
Lemmas hooded.
Kernels white, blue, or purple . . . . . 31. *sublaxum*
Kernels black . . . . . 32. *gymnospermum.*

For further divisions within the thirty-two varieties, Harlan used width of the outer glume, color of the kernels, character of the awns, density, and width and attitude of spike, in the order named. Thus, density, which has been given such an important place in all previous classifications, is here used only for a minor varietal distinction. No attempt is made in this publication by Harlan to distinguish commercial varieties.

NUMBER OF SPECIES

Although there is a consensus of opinion that fertility should be used as one, if not the only, character in making up the main groups of barley, there is by no means the same harmonious agreement in regard to the number of species. On the one hand, there is a group consisting of Linnaeus (1753), Schübler (1818), Séringe (1819), Carleton (1916), and Harlan (1918), who have considered cultivated barleys as forming from three to seven species; on the other hand, Jessen (1855), Körnicke (1885), Voss (1885), Atterberg (1899), and Munro and Beaven (1900), have preferred to group all barleys under one species.

In general, species in cultivated crops should be based on their origin, as far as is possible. This general rule cannot be followed absolutely because of the uncertainty in regard to the progenitors of many groups of plants. After the species have been established, the subspecies and the groups should if possible be based on the order of evolution. This, like the establishment of the species, is uncertain to a large degree, and thus the classification becomes more and more artificial.

In the establishment of species in the case of barleys, the very earliest classifications cannot have much weight because of the smallness of the

ollections and the lack of research in regard to their origin. Körnicke as the first to present the theory that all domesticated barley originated rom one wild species, *Hordeum spontaneum*, and on this basis he made ne species, *Hordeum vulgare*. Jessen, however, had previously considered ll barley to belong to one species, *Hordeum sativum* Jess. Voss, Atterberg, nd Beaven, following Körnicke's theory, considered barley as only one pecies but followed Jessen in terminology. In more recent years conderable evidence has been produced which indicates at least two wild ncestors for cultivated barley. The best discussion of this subject is y Schulz (1913), who presents the theory that by the accumulation of everal small variations from the wild species *H. spontaneum*, a new ild species, *H. ischnatherum*, was produced which is widely distributed the Tigris-Euphrates region. This form as it is found presents several ariations in the characters of side spikelets, just as does the wild species . *spontaneum* but in general it is much nearer the six-rowed type than *H. spontaneum*. Schulz offers the further theory that by the accumulation still more variations from *H. ischnatherum*, the cultivated forms of the x-rowed barleys have been derived, and in a similar manner the cultivated rms of the two-rowed barleys also have been derived from *H. spontaneum*. is opinion in regard to the origin of the intermediate forms between e common six-rowed and the common two-rowed barleys is that they ose by crossing. He thinks that the deficient forms arose directly from . *spontaneum*, and not from any cultivated forms of two-rowed barleys.

SUMMARY

From the foregoing review of the various classifications, the progress ter Linnaeus may be briefly summarized as follows:

1. The division of *Hordeum distichon L.* into *H. erectum* and *H. nutans* Schübler.
2. The grouping of all barley varieties into one species by Jessen.
3. The conception of the variety as a unit, by Körnicke, and the establhment of a large number of varieties on a firm basis. (Körnicke's main oups, however, were not an improvement over the groups previously ablished.)
4. The new system of Atterberg, whereby 188 varieties were designated the use of 33 terms. (It is doubtful whether this was an advance.)

SUMMARY TABLE SHOWING THE DIFFERENT USE OF CHARACTERS BY VARIOUS INVESTIGATORS IN THE CONSTRUCTION OF THEIR KEYS

Rank	Linnaeus 1748	Schubler 1818	Kornicke 1885	Voss 1885	Neergaard 1889 and Bohn 1893	Atterberg 1899	Beaven 1902	Carleton 1916	Harlan 1918	Proposed ranking
1	Fertility	Fertility	Fertility	Fertility	Fertility	Terminal appendage	Fertility	Fertility	Fertility	Fertility
2	Density	Density	Terminal appendage	Shape of spike	Shape of kernel	Outer glumes	Width of spike	Color of grain	Adherence of lemma	Adherence of lemma
3	Adherence of lemma	Adherence of lemma	Number of rows or ranks	Arrangement of spikelets	Rhachilla	Adherence of lemma	Length of internode	Shape of spike	Terminal appendage	Terminal appendage
4			Adherence of lemma	Color of spike	Lateral nerves	Color of grain	Adherence of lemma	Terminal appendage	Color of kernel	Color of kernel
5			Outer glumes			Fertility	Color of grain	Early habit of growth	Outer glume	Density
6			Color of spike			Length of internode	Rough or smooth awns		Color of kernel	Rhachilla
7			*Length of kernel			Width of spike	Outer glumes		Rough or smooth awns	Rough or smooth awns
8			Length of spike			Attitude of spike	Rhachilla		Density	Early habit of growth
9			Rough or smooth kernel			Base of kernel			Width of spike	Lateral nerves
10			Rhachis			Rhachilla			Attitude of spike	Shape of spike
						Rough or smooth awns				Color of kernel

5. The classification of cultivated varieties by Beaven, wherein the treatment of the main groups was superior to that of Körnicke.

6. The discovery by Neergaard of the stability of the long- and the short-haired rhachillas, and the smooth and the barbed lateral nerves.

7. The researches of Harlan in regard to pigmentation in barleys.

8. The reclassification of barleys by Harlan wherein the main groups were established on the basis of fertility alone.

The relative weight given the different characters by the various investigators are summarized in the table on the opposite page. It is seen that there is a very marked lack of agreement in the use of the various characters for classification purposes, with the one exception of fertility, which is used as a basis of separation for the main groups or species in every case but one.

MATERIAL USED IN THE PRESENT CLASSIFICATION

In the present study 627 specimens were under observation, many of which were alike in name and in all observable morphological characters. These so-called varieties were largely collected in 1915 by Professor E. G. Montgomery, of Cornell University, for the purpose of classification. The most valuable individual collections were those obtained from the California Experiment Station at Berkeley, California, the E. Clemens Horst Company of San Francisco, and the Ökonomisch-botanische Garten of Halle University in Germany. From these three sources alone an aggregate of 475 specimens were obtained, including all the types of any economic importance and practically all the rarer types. This original collection has been enlarged by additions from the Department of Plant Breeding at Cornell University, from the Office of Foreign Seed and Plant Introductions and the Office of Cereal Investigation of the United States Bureau of Plant Industry, from the state agricultural experiment stations, particularly those of Virginia and Wisconsin, and from other minor sources, all of which have aided materially in completing the collection.

The collection has been in the hands of the writer since 1915 and has been grown each year in rod rows, one foot apart. Since yield was not a factor in the present study, the rate of planting was adjusted in all cases so that good development of individual plants might be obtained

MORPHOLOGY OF THE BARLEY PLANT

The first thing necessary in making a key for a group of plants is a detailed study of the morphological characters of the plants. This study is necessary for two reasons — to acquaint the investigator with the plants with which he expects to work, and to learn the characters that are not influenced by environmental conditions. These are the characters that must be given the important places in the classification. Therefore a consideration of the morphological characters is of much importance in this paper. The various discussions herein not only include a description of the individual characters, but also consider their value taxonomically and the use made of them in the present and in previous classifications. However, the relative taxonomic value of the various characters is not given any weight in the arrangement of this section.

The morphological characters as discussed herein are divided into three groups and are treated according to the following order: gross characters, spike characters, and spikelet characters.

GROSS CHARACTERS

The gross characters of barley, which include color, shape, and size of the leaves, number and size of culms, roots, and some other characters, are the least valuable among the three groups of characters from a taxonomic standpoint. The differences in these characters are usually not sufficient to warrant taxonomic divisions. Furthermore, they are the most variable of all the characters under different environmental conditions. Their chief value is to be found in varietal descriptions.

Foliage

The foliage of barley varieties presents a rather wide range of variations, all of which are difficult not only to describe but also to recognize. Variations occur in color, length, width, and number of leaves. Kornicke (1885), in his varietal descriptions, used four shades of green — bright, dark, bluish, and yellowish. Difficulties immediately arise in such descriptive terms, because the personal factor is too great in describing or recognizing such a character for it to have much value. Other investigators have recognized difficulties in using such characters, and as a

consequence have used color of foliage with much precaution. The length and the width of the leaves are variables which, like color, are largely dependent on environment and are limited in their use in the same way. For them to be of any value, accurate statistical work must be done. As a rule, when significant differences are found, it is between the larger groups, where no such detailed observations are necessary for the distinction. The most marked variation in leaves is between the spring and the winter barleys, which are discussed later. The variation in the number, exclusive of the basal leaves, is identical with the number of nodes, which is discussed in connection with culm characters.

Culm characters

The culms of barley vary in several characters, but, in general, greater variations are produced by different environments than exist between closely related forms. For this reason these variations are, like the variations in the foliage, of minor importance in classification. Their only value is in varietal description. Such characters as height of the plant, number of culms to the plant, diameter of the culms, thickness of the culm wall, number of nodes, and length of the last internode, have been used more or less extensively in descriptions. Körnicke (1885, 1895, and 1909) made use of many varying vegetative characters in descriptive work.

Height of plant

The height of certain varieties in a particular locality varies as much as 100 per cent and for this reason may be of importance locally, but these same varieties grown in another region may have a reverse relationship in regard to height. This has been well shown by Harlan, who in 1911 selected thirteen pedigreed barleys representing a wide range of types and planted them at four widely separated points. He found a marked regional response For example, Odessa was short and unpromising in Minnesota and little better in California, but was very tall and vigorous in both Montana and North Dakota. The Abyssinian varieties, on the contrary, grew well in California but were very short elsewhere, as is seen from the accompanying table taken from Harlan (1914):

INFLUENCE OF GEOGRAPHICAL LOCATION ON THE LENGTH OF THE CULM IN 12 REPRESENTATIVE SELECTIONS OF BARLEY GROWN AT FOUR WIDELY SEPARATED POINTS, THE SELECTIONS BEING ARRANGED IN THE ORDER OF THEIR HEIGHT AT EACH POINT

St. Paul, Minnesota	Williston, North Dakota	Moccasin, Montana	Chico, California
Hordeum vulgare	Servian	Odessa	S. P. I. No. 20375
Oderbrucker	Odessa	*Hordeum vulgare*	Oderbrucker
Manchuria	*Hordeum vulgare*	Surprise	Abyssinian
Summit	Smyrna	Summit	Servian
Princess	Oderbrucker	Servian	Smyrna
Surprise	Manchuria	S. P. I. No. 20375	Manchuria
Servian	Summit	Kitzing, 6-rowed	Summit
S. P. I. No. 20375	Surprise	Manchuria	Odessa
Kitzing, 2-rowed	Kitzing, 6-rowed	Oderbrucker	Kitzing, 6-rowed
Kitzing, 6-rowed	S. P. I. No. 20375	Smyrna	Princess
Abyssinian	Princess	Abyssinian	Kitzing, 2-rowed
Smyrna	Abyssinian	Kitzing, 2-rowed	Surprise
Odessa	Kitzing, 2-rowed	Princess	*Hordeum vulgare*

Length of last internode

The relation of the spike to the leaf sheath depends entirely on the length of the last internode — the one on which the spike is borne. The shorter the last internode, the less the spike will be exserted. The failure of the spike to be exserted from the leaf sheath has been used repeatedly in describing such barleys as the Smyrna and Princess varieties. The fact that this character occurs in the same varieties in widely differing localities is evidence enough that it is a true varietal character, but there is considerable variation within the variety. It is, however, characteristic enough in a few instances to determine a variety. In the present classification the length of the last internode is used in varietal descriptions.

Number of nodes

The number of nodes varies from three to seven in different varieties, but in all cases there is sufficient variation within the varieties to cause an overlapping, thus making the character uncertain. The number of leaves to a culm is identical with the number of nodes and consequently varies in the same way.

Roots

So far as it was determined, there are no varietal differences of roots that can be employed in classification. The ratio between top- d roots

may vary to some extent between varieties, but similar variations occur within the variety as a result of local conditions. Consequently, root characters are of no value either for classification or for descriptive purposes.

Habit of plant in early growth

The habit of the plant in early growth is very important because it is by this character that spring and winter varieties are separated. The difference appears both in the number and the attitude of the culms and in the number of leaves. The ordinary spring varieties of barley have a small number of culms which stand erect at all stages of growth, and only a few basal leaves. Winter varieties, on the other hand, have a large number of culms and leaves which are more or less decumbent during the early part of the development of the plant. It is at this stage that such varieties pass the winter period. In the spring, when new growth begins, a few of the many culms elongate, producing the flowering stalks and the grain of the plant, while the others remain undeveloped and sooner or later disappear as a vital part of the plant.

If these same varieties are seeded in the spring, a large tuft of leaves and very short culms are produced early in the season. The plants will remain at this stage for a considerable period before the flowering stalks are produced; in some cases, in fact, the flowering stalks entirely fail to appear, while those that do appear are usually infertile or produce very little grain. For this reason, it seems that a dormant period is needed for the proper development of these varieties.

An intermediate condition, which may be called *semi-erect*, is also found in some varieties, in which the number of culms and leaves is above the average for barleys and the culms tend to spread out to some extent. All of such varieties are, however, spring varieties. This character can be used only in varietal description.

The distinction between winter barleys and spring barleys was made by Kornicke (1885) and by Carleton (1916) in describing varieties, but has never been used as an important distinction between large groups of varieties. In the present classification the habit of the plants in early growth is used only in minor separations.

Emergence of awns and spikes

The date at which the head appears is a note that has been generally taken by all barley breeders as well as by those studying varietal differences. More recently this has been replaced by a note on the date of appearance of the awns. Harlan (1914) showed that the latter is more nearly accurate and easier to obtain than the former. This has proved to be true in the present investigation. The only objection to using the date of the emergence of the awns, instead of the date of the appearance of the head, is that hooded and awnless varieties cannot be compared with awned varieties. This is not a serious objection, however, as this character can be used only to distinguish strains within a variety. The relationship of strains in this regard varies with the locality. In the few cases of awnless and hooded varieties, it is necessary to use the date of the appearance of the spike as the distinguishing character. The date of appearance of either the awn or the spike is so variable that it has no taxonomic value.

Time of maturity

Ordinarily the time of maturity is correlated with the date of emergence of the awns, but, as is the case with most other correlated characters, some exceptions occur. This character is of value at times, not only in distinguishing different varieties or strains in a given environment, but also in detecting mixtures in the field. A pure strain will mature all spikes within a very few days. This character is much more reliable when used in connection with early-maturing than with late-maturing varieties. Late-maturing varieties are often ripened abnormally by unfavorable weather conditions. This character is used in the present classification only in distinguishing strains otherwise similar, and in varietal descriptions.

Production

The yield of varieties, although in a given region varying from very small to very large, cannot be employed for classification purposes because it is almost wholly dependent on environment. Consequently, production has no place in the present investigation.

SPIKE CHARACTERS

The characters of the spike, including variations in fertility, density, and rhachis, are far more important from the standpoint of classification

than the gross characters already discussed. Some of these spike characters which are the most conspicuous and the easiest to recognize, have been used in all previous barley classifications. In most instances either density or fertility has been given first place in the formation of groups.

The differences in the characters of the spike are great and have been found to be constant under different environmental conditions. Because of these facts they have proved to be of much taxonomic value, and are so considered in the present classification.

Fertility

Barley varieties, as stated above, have been divided into groups according to the fertility of the spikelets, by all investigators who have worked on their classification. The first pre-Linnaean divisions were made on this character when only two groups were recognized, the two-rowed and the six-rowed. Linnaeus likewise followed this scheme, but used in connection with it the density of the spike, thereby making four groups or species. In 1885 Steudel (cited by Körnicke, 1885) fully described a third degree of fertility, which he designated as *deficiens*. Körnicke (1885) recognized a fourth degree of fertility in his group, known as *intermedium*. Thus, four definite stages of fertility have been recognized as important in the formation of groups in the case of barley.

In order to understand the variation in fertility, it is necessary first to know the structure of the barley head. Barley, in common with all other members of the genus Hordeum, produces three single-flowered spikelets at each node of the flattened rhachis. Structurally the spikelets are very similar, each having two outer glumes, a lemma, and a palea, which inclose the sexual organs. In all cultivated barleys, the central spikelet of the series of three at each internode is always fertile. The variation in fertility is found only in the side spikelets, which present four stages of fertility, as has already been stated. These different conditions of fertility are as follows: (1) all three spikelets equally fertile, with the lemmas of each projected into a terminal appendage, either an awn or a hood as the case may be, and with the kernels of the side spikelets almost as large as the kernels of the medium spikelets (fig. 51, A and B, and fig. 69, *H. vulgare*); (2) all three spikelets fertile, but the lemmas of

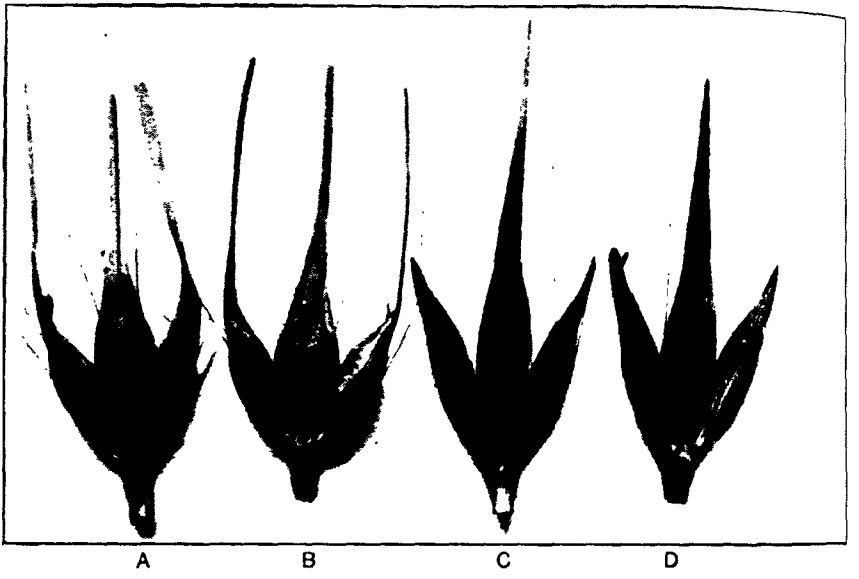


FIG. 51. THE STRUCTURE OF SIX-ROWED BARLEYS

A, Dorsal view of perfect condition of fertility, where all spikelets are equally fertile and awned; B, ventral view of same; C, dorsal view of second condition of fertility, where side spikelets are fertile but about one-half the size of median spikelets and not awned; D, ventral view of same

the side spikelets without terminal appendages, ending either in a point or bluntly, and the kernels of the side spikelets about one-half the size of the kernels of the median spikelets (fig. 51, C and D); (3) the side spikelets infertile, but possessing rudimentary sexual organs and all the structural parts of the fertile spikelets except the terminal appendages of the lemma (fig. 52, A and B); (4) the side spikelets infertile, without rudimentary sexual organs and with all structural parts very much reduced. In some cases, only the two outer glumes and a rudimentary rhachilla remain as evidence of the side spikelet (fig. 52, C and D). The relative position and size of the spikelets in the various types is diagrammatically shown in figure 53.

These four conditions of fertility, previously recognized, have remained practically stable since they were first described. For this reason, and because they have been constantly used in all early classifications, they

are of the greatest taxonomic value. Some intermediates between these stages have been described from time to time by different authors, especially Körnicke (1885). Most of these which were the results of crosses have proved to be unstable and have gone out of existence as varieties. Crosses between two of the above-named conditions of fertility give in the second generation practically all steps between the two parent types, but these intermediates have proved heterozygous in future generations and have broken up in a similar manner to the original first-generation cross.

In the present classification, these four conditions of fertility are used as the first and most important character in the subdivision of cultivated barleys, for three reasons: (1) stability in all environmental conditions; (2) ease of recognition; and (3) weight given by all earlier investigators.

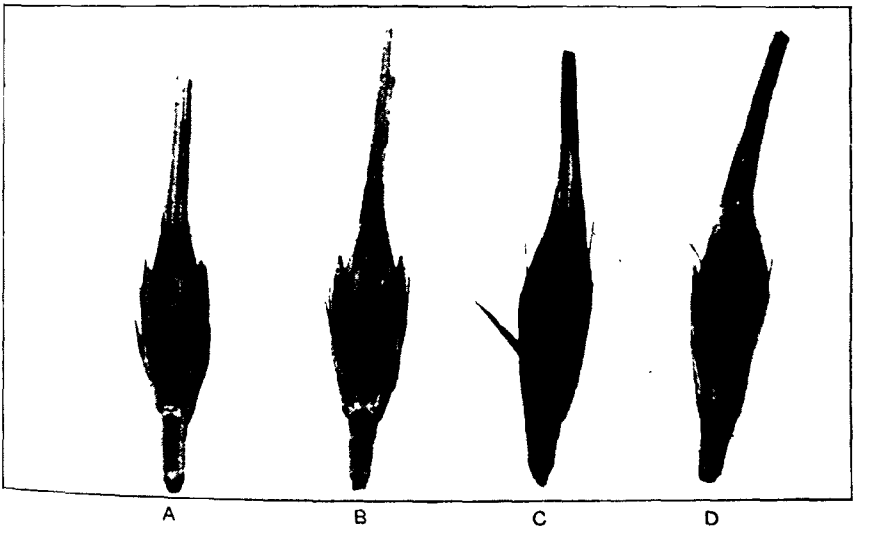


FIG. 52. THE STRUCTURE OF TWO-ROWED BARLEYS

A, Dorsal view of third condition of fertility, where side spikelets are infertile but possess all structural parts except terminal appendage of lemma; B, ventral view of same; C, dorsal view of fourth condition of fertility, where side spikelets are very rudimentary; D, ventral view of same.

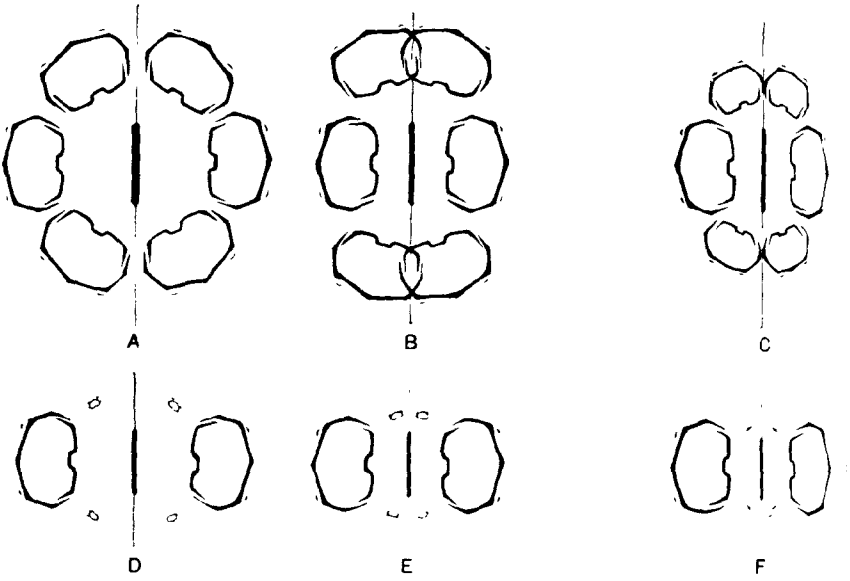


FIG. 53. DIAGRAMMATIC SKETCH OF CROSS SECTIONS OF SPIKES OF VARIOUS TYPES OF BARLEY
A, *H. vulgare* (dense form; B, *H. vulgare* (lax form), C, *H. intermedium*; D, *H. distichon* (dense form); E, *H. distichon* (lax form), F, *H. deficiens*

Branch-headed barleys

One other structure sometimes arises in barleys, which has caused descriptions to be written of what were termed *seven-rowed, eight-rowed,* or *nine-rowed barleys.* Such a condition, which might be called a stage of fertility, is brought about by repetitions of the three spikelets at a node. In other words, instead of one series of three spikelets at each node of the rhachis, there are three series (fig. 54). In the case of the two-rowed barleys, if this occurs regularly a six-rowed barley would be produced, but instead of only three spikelets at one internode, all of which were fertile, there would be three fertile and six infertile spikelets. If the same thing were to happen in the case of the six-rowed barleys, an eighteen-rowed barley would result. At each node of the rhachis nine kernels would appear. No instances have been reported in which there was such a replication at every node. The change usually comes at or near the base of the spike, and at only a small number of nodes. A further deviation occurs when a true branch is formed which bears spikelets at

each internode just as the main axis of the spike does. These likewise arise near the base of the spike.

Occasionally such deviations as are mentioned above are more or less constant, but more often they are found to be variable, due to environmental conditions. In either case they have no economic importance and very little taxonomic value. Consequently they are not used in the present classification as characters of importance in separating groups or even varieties.

Density

The density of the spike in barley, by which is meant the number of florets to the unit length of rhachis, has been employed by all taxonomists in the classification of barleys, in one form or another. In the greater number of cases it has been given equal weight with fertility in the formation of either species or subspecies. In fact, density has been considered by many authors as a result of varying degrees of fertility. This, however, can easily be disproved by making comparative weights of the kernels of the lateral and central spikelets of either common or erect six-rowed varieties. There is just as much difference between these two groups of spikelets in the erect varieties as in the common. The groups according to density have generally been divided into dense and lax forms. For the sake of varietal description Koernicke (1885) even mentioned a division of the dense forms into dense and very dense.

FIG. 54. TWO-ROWED BARLEY

A, Spike of branch-headed two-rowed barley; B, one internode of the rhachis with its abnormalities

It was not until Atterberg (1899) presented his new system of classification that the density of the spike was made a character of minor importance. In the earlier works, density and fertility were given about the same weight. In Atterberg's new system, density was considered only after the characters of terminal appendage, outer glume, fertility, and side spikelets.* Following Atterberg, both Beaven and the investigators at Svalöf went back to the old system of considering fertility and density as practically of equal importance. In Harlan's recent paper (1918), density is again employed only as a distinguishing characteristic between subvarieties.

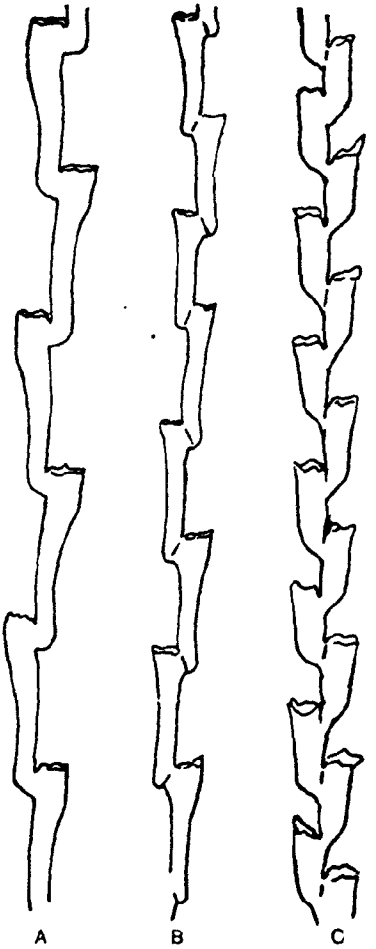


FIG. 55. RELATIVE LENGTH OF RHACHIS INTERNODES OF BARLEY OF DIFFERENT DENSITIES (× 6)

A, Lax; B, erect; C, very dense

That there is a decided variation in this character of the spike in barley varieties cannot be denied. The difficulty in the use of this character lies in the intergradations between the dense and the lax forms. In a large collection of barleys it is possible to find practically all degrees of density, from the very lax to the very dense. This difficulty has been mentioned by earlier writers. Körnicke, however, based his several subdivisions on the variation in the density of the spike. In the present classification, density is used in the separation of rather large groups of commercial varieties but is not considered as important as either fertility, adherence of glumes to the caryopsis, terminal appendage, or color.

Length of internodes of rhachis.—The length of the internodes of the rhachis varies directly with the density, and is the deciding factor in, density. The character

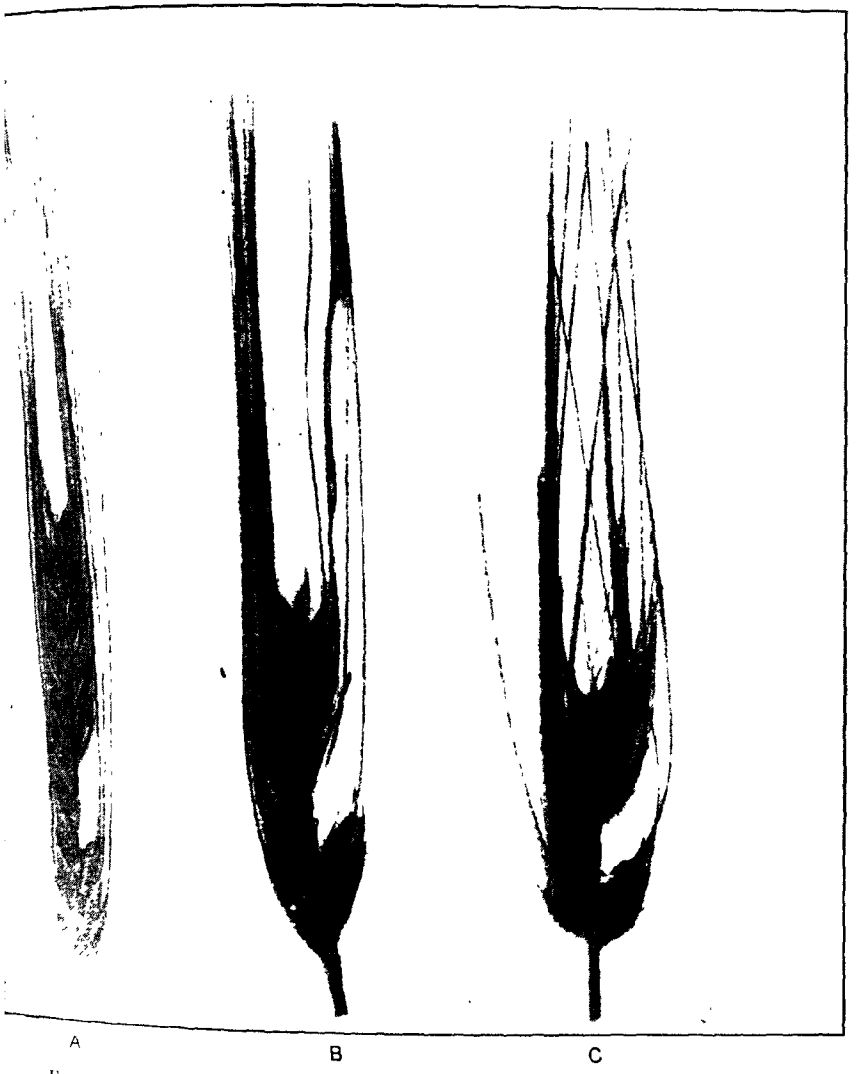


FIG. 56. VARIATION IN THE ANGLE OF INCLINATION OF KERNEL WITH RHACHIS
A, Chevalier; B, Goldthorpe; C, Fan barley

has been used in the determination of density by several investigators, especially Atterberg (1899) and Harlan (1914). Atterberg used the average length of the internodes as the chief character in separating his subvarieties. In the present classification, the length of internodes has been found very useful. In two-rowed forms, three quite distinct groups were found centering around the lengths 3.3, 2.5, and 1.7 centimeters to ten internodes, or, in other words, giving a ratio of almost 2:1.5:1 (fig. 55). In the six-rowed forms the very dense group was not so distinct. Variations from the general averages were found in many cases. These lesser variations can be used only in descriptions of varieties under like environmental conditions, and would not necessarily hold if the specimens were grown in different localities. The larger differences, however, are little influenced by environment and can consequently be used in classification with a considerable degree of certainty.

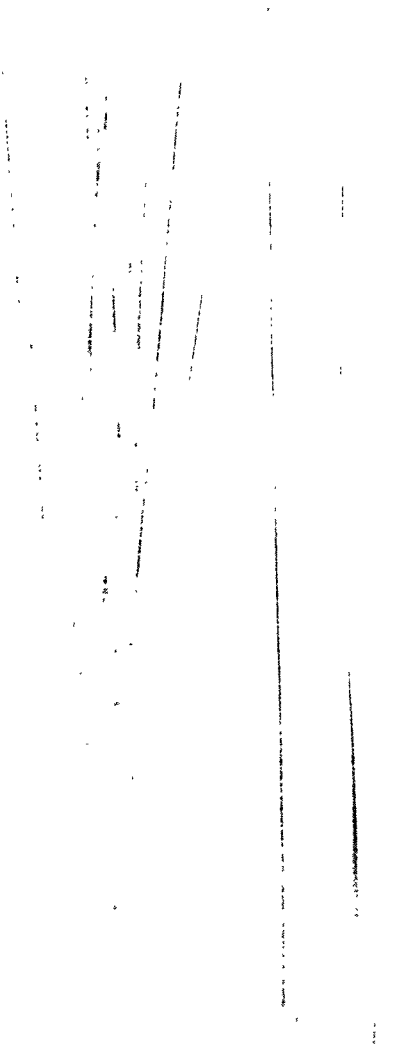
FIG. 57. VARIATIONS IN THE ATTITUDE OF THE SPIKE IN LAX AND DENSE FORMS

Angle of inclination of kernel

The angle of inclination of the kernel is only another expression of density. It increases directly with the density and inversely with the length of the internode. The shorter the internode, the greater is the angle of inclination of the kernel (fig. 56). This character is, however, harder to determine and less accurate than the length of the internode. For this reason, length of internode is given preference in the present study in the determination of density. The angle of inclination, nevertheless, has been used by the Svalöf investigators in describing varieties.

Attitude of spike

The variations in the attitude or the relative position of the spike in regard to the culm, some of which are shown in figure 57, are likewise closely correlated with the length of the internodes of the rhachis, and for this reason may be disregarded in most cases. They are of value in descriptions of varieties and in the comparison of widely different types. One advantage which this character in its extreme conditions has over the length of the rhachis internodes is that of ease in determination. It is not reliable, however, except under very favorable growing and ripening conditions, and is used in the present classification only in connection with the



A B

FIG. 58. HORDEUM SPONTANEUM

A, Entire spike; B, one internode of rhachis with spikelets attached

length of the internode. This character has been used in connection with density by practically all previous investigators.

Articulation of internodes of rhachis

In the wild types of barley known at present, the rhachis separates at maturity into as many segments as there are internodes in the rhachis. This separation is by disarticulation and not by rupture (fig. 58). Each separate segment remains attached to one spikelet. In the cultivated types of barley this separation does not take place; the rhachis either remains entire, or, if threshed, may be broken to pieces by rupture but seldom by disarticulation. In either case, however, no part of it remains with the spikelets. Nevertheless, there is considerable variation in this character of the rhachis in cultivated barleys. Although no part of the rhachis remains with the threshed grain, there is a tendency in certain varieties for the rhachis to separate easily into the various segments at maturity. This difference is a matter of degree, and as a consequence cannot be used as an important taxonomic character. But it has considerable value in varietal distinctions, and is used in that connection in the present paper.

This character has not been used by previous investigators either as a group characteristic or as a varietal difference.

SPIKELET CHARACTERS

The spikelet in the case of barley presents several characters which are very important from the standpoint of classification, second only to the two principal spike characters already discussed. The most valuable spikelet characters in barley are those of the caryopsis, the glumes, and the rhachilla. These present wide differences, many of which have been found to remain constant under all environmental conditions. They have found second place in classifications because of difficulty in determination, and in some cases of intermediacy

The grain

The term *grain*, as used in this paper, when applied to hulled barleys includes both the caryopsis and the adhering lemma and palea; but when the term is applied to hull-less varieties, only the caryopsis is con-

sidered. In other words, *grain* is the term applied to the threshed product. The grain of barley presents several important characters, both commercially and taxonomically — composition, size, shape, and color.

Composition

The composition of barley grain of the hulled varieties is a subject that has been given much study in connection with malting. The composition of hull-less varieties has not, however, been given equal consideration. For this reason, and because the same variations occur in each form, data for only the hulled type are given herein. Beaven (1902), and Le Clerc and Wahl (1909), report a large number of analyses of barleys. From these data it is apparent that composition is influenced much more by environment, rainfall, temperature, sunshine, and fertilizers, than by the variety. The following table from Le Clerc and Wahl illustrates this fact:

Variety and State	Water (per cent)	Fat (per cent)	Fiber (per cent)	Starch (per cent)	Protein (per cent)	Hulls (per cent)	Weight of 1000 grains (grams)	Ash (per cent)
Bay Brewing								
California	8 23	2 06	6 72	58 23	9 77	14 16	35 82	3 03
Kansas	10 32	2 02	7 31	59 66	13 69	15 00	30 56	3 41
Two-rowed								
California	8 82	2 15	5 52	60 38	10 66	11 08	35 28	2 72
Kansas	10 09	2 23	5 38	55 91	17 69	11 70	35 07	3 13

The difference in the composition of the same variety in different localities is much greater than the difference in the composition of different varieties in the same locality. This is especially true of water, protein, and ash contents. These data verify previous work along the same line. Regardless of this truth, there is a strong tendency for some varieties to possess heritable differences in composition. This character may in some instances be used in differentiating varieties that are grown under exactly the same environment, but in a classification of barley varieties it has little place. In the present investigation the composition of the grain is not used.

Size

The average size of the grain has been used by agronomists generally in describing varieties and strains, but the differences are usually very

small in closely related samples, making its value doubtful. It is, however, more significant in the case of widely different groups. But in such instances other more reliable and less variable characters are usually present. For these reasons, and because it varies greatly with the environment, it is used in the present classification only in varietal descriptions.

The variation of the size of grain within a variety may, however, be significant as an aid in determining the groups to which a variety belongs, if the sample is threshed. All grains are of approximately the same size in the two-rowed groups, while in the six-rowed groups one-third of the grains are noticeably larger than the other two-thirds, and in the intermediate group one-third are approximately twice the size of the other two-thirds. These distinctions are valuable only in connection with threshed grain. In the case of threshed samples of hull-less types, this variation in size may be the only way of distinguishing two-rowed from six-rowed varieties. With threshed samples of hulled types, however, the shape of the grain, as described later, is more reliable in determining groups.

Shape

The difference in shape of the grain between the two-rowed and the six-rowed hulled types has become well established as a group distinction (fig. 59). The grains from the lateral spikelets are all more or less twisted in the six-rowed varieties, while those from the central spikelets are all symmetrical in contour. In the two-rowed varieties all the grains are symmetrical in contour, since they are produced by the central spikelets. There is a difference even between the shape of the grains of the two-rowed varieties and the grains of the central spikelets of the six-rowed varieties. The grains of the central spikelets of the six-rowed varieties are broadest near the tip, while those of the two-rowed varieties are broadest near the base. This difference has been used by the Swedish investigators as a group distinction, and is used in the present investigation only for a study of threshed grain. It has no value in identifying threshed samples of hull-less barley, because all grains are symmetrical, due to lack of compression by the glumes.

The differences in shape to be found between varieties in the lesser groups are very small and must be based on measurements of the various

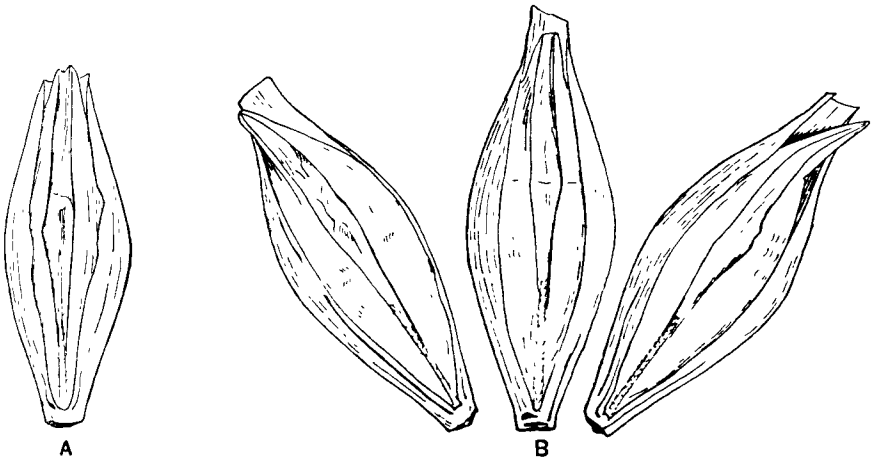


FIG. 59. DIFFERENCE IN APPEARANCE OF VENTRAL VIEW, OF GRAIN OF TWO-ROWED BARLEY AND OF GRAIN OF LATERAL SPIKELETS OF SIX-ROWED BARLEY

A, Grain of two-rowed barley; B, grain of lateral spikelets of six-rowed barley

dimensions. The most reliable and least influenced by environmental conditions, as found by Harlan (1914), is in length. By this measurement it is possible in a few instances to distinguish between certain very similar varieties or strains. This character is used only in varietal description in the present classification.

Color

The color of both the caryopsis and the glumes (lemma and palea) has been used in practically all classifications that have appeared. The use, however, has not been consistent, probably because the nature of the pigmentation of barley was not understood. The following colors have been used in classifications by various investigators: white, yellow, black, violet, purple, and blue-gray. The use of color by Beaven (1902) may be given as a typical instance:

Colour of (1) the paleae*; (2) the seed (caryopsis).
(a) Yellow or white paleae and seed.
(b) Yellow or white paleae with bluish-grey seed.
(c) Brown paleae.
(d) Black paleae. The colour of the seed (caryopsis) when naked in the two latter cases also varies.

*Beaven used the term *paleae* to include both lemma and palea.

It remained for Harlan (1914) to make a detailed study of the pigmentation of barleys. This work has aided materially in giving an understanding of the variations in color, and in clearing up inconsistencies. As a result of his work, Harlan found that all pigmentation was the result of only two pigments, anthocyanin and a melanin-like pigment. He found four color conditions to exist as a result of the total absence or the different location and combination of the pigments, as follows:

1. (a) Hulled varieties without pigment in either lemma or aleurone layer.
   (b) Hull-less varieties without pigment in the aleurone layer or in the pericarp.
   Either of these conditions results in a white or a yellow barley.
2. (a) Hulled varieties with a blue aleurone layer showing through the superimposed lemma.
   (b) Hull-less varieties with a blue aleurone layer showing through a pericarp containing no pigment.
   Either of these conditions results in a blue barley.
3. (a) Hulled varieties with purple lemmas.
   (b) Hull-less varieties with blue aleurone and red pericarp.
   Either of these conditions results in a purple barley.
4. (a) Hulled varieties with black lemmas.
   (b) Hull-less varieties with black pericarp.
   Either of these conditions results in a black barley.

Another color condition sometimes appears in immature white or yellow barleys. The lack of maturity causes the development of a greenish color which is probably not due to any pigment. The blue and purple color conditions mentioned above are due to one pigment, anthocyanin. In an acid condition this appears red and in an alkaline condition it appears blue. The combination of the two produce purple. The black color is due to the melanin-like pigment, which is unchanged by treatment with either an acid or an alkali. The brown color as used in some classifications is without doubt a black, and consequently has in most cases, if not in all, very little taxonomic value.

Color as used in the present classification follows the grouping as given above. Because of the ease of recognition and the distinct condition of color, it is given an important place herein in making the various groups. The blue condition is the only one which is at times difficult to recognize. In the case of hulled barleys, the color may be obscured by weathering

at harvest time unless conditions are very favorable. In these instances it is necessary to remove the glumes in order to detect the color. If there is still doubt in regard to the presence or the absence of the blue pigment, the question may be determined by a simple chemical test which consists in dropping into a weak acid solution some kernels whose seed coats have been cut through. In a few minutes, according to the strength of the solution, a pink ring will appear in the region of the aleurone layer if any pigment is present; if no pigment is present there will be no color.

If barleys under study are immature, another difficulty may arise in determining color, since pigmentation is developed in the last stages of maturity. If harvest takes place too soon the development is somewhat arrested, and this may cause difficulty.

Pigmentation likewise occurs in other parts of the plant, particularly in the leaves and the stems. The pigment concerned is usually, if not always, anthocyanin. The appearance of coloration is, however, not normal in most cases and is never reliable as a taxonomic character. It usually appears as a result of arrested development, hastened maturity, or other abnormal conditions due to malnutrition.

The lemma,[6] *or flowering glume*

No other single structure in barley gives so many morphologically important characters as does the lemma. Some of the characters of this structure have been used by all investigators who have attempted either classifications or descriptions since the time of Linnaeus. Their relative importance has not been the same in all cases, but without exception the separation of large groups has been made by the use of one or more of the lemma characters.

The color of the lemma has already been discussed in connection with the color of grains, and need only be mentioned here. The remaining important lemma characters, the variations of which are constant in different varieties or groups, are the adherence of the lemma and the palea to the caryopsis, the terminal appendage, the number of nerves, the barbing of the lateral nerves, and the base. These characters are discussed in the above order.

[6] The [illegible] *lemma* is used throughout this paper instead of the term *flowering glume*. Not only is *lemma* shor[illegible] than *flowering glume*, but it serves to distinguish this structure from the outer glumes of [illegible] It is also the term now commonly used by agronomists. It is, however, morphologically [illegible] outer, or empty, glumes, all of which are reduced structures on the main axis of the spikelet, [illegible] from the other glumes of the spikelet by arising from the secondary axis of the spikelet

Adherence of lemma and palea to caryopsis

Two very different and easily distinguishable conditions exist in regard to the adherence of the lemma and the palea to the caryopsis. The condition that is probably the more characteristic and the more primitive is the one in which both the lemma and the palea are grown fast to the caryopsis at maturity. This union takes place near the time of maturity, when the caryopsis has reached its maximum size. Varieties with this characteristic are known as hulled barleys. In contrast to these, some varieties fail to form a union between the lemma and palea and the caryopsis. In such cases the caryopsis at maturity is easily separated from the lemma and the palea. Varieties with this characteristic are known as hull-less, or naked, barleys.

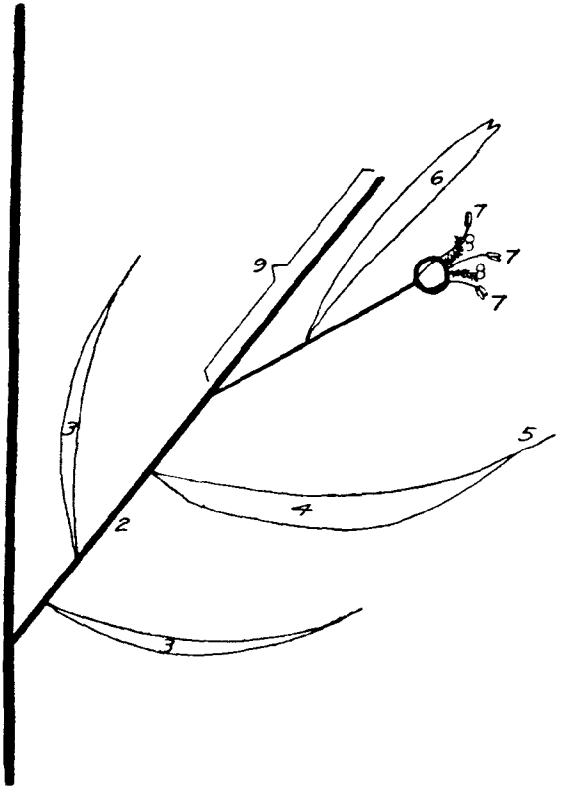


FIG. 60. DIAGRAMMATIC SKETCH OF BARLEY SPIKELET

1, Rhachis, or primary axis of spike; 2, primary axis of spikelet; 3, outer glumes; 4, lemma of flowering glume; 5, awn; 6, palea; 7, stamens; 8, pistils; 9, rhachilla

These contrasting characters were first recorded by Linnaeus (1753). By their use he made two groups each of lax six-rowed and lax two-rowed barleys, but did not consider them sufficiently important for the establishment of species. They have since been used in all classifications as important taxonomic characters.

There is never any question in determining this character in mature grain because intermediates do not occur. Even in crosses the intermediate condition is not found, a fact which is not true with many other characters in hybrids. No established variety from crosses of hulled and hull-less types shows intermediacy. Because this character can be readily observed both in threshed and in unthreshed grain, and because of the total lack of intermediates, it is second to no other character taxonomically; but because of precedence and the probable evolutionary development, it is given second place in the present classification.

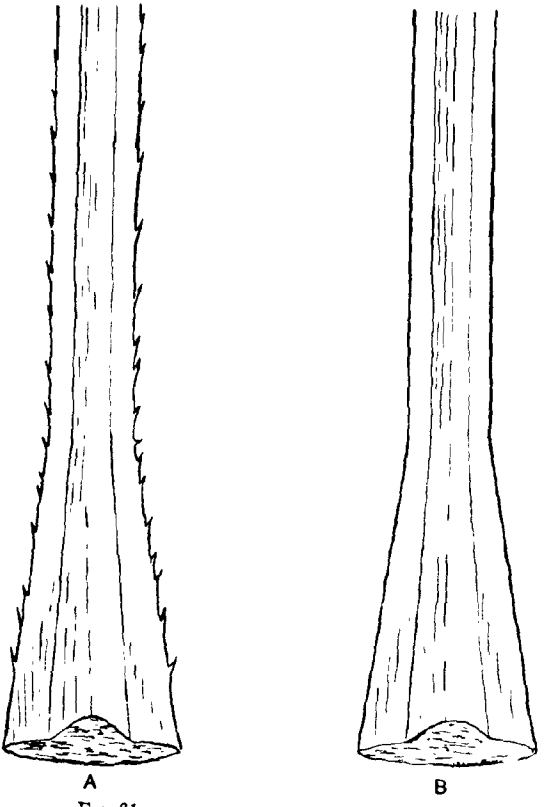


FIG 61. VARIATION IN BARBING OF AWNS
A, Barbed; B, smooth

Terminal appendage

The terminal appendage of the lemma in barleys may be divided into three types: the normal, or awned (fig. 66), the awnless (fig. 68), and the hooded (fig. 67, B and D).

The normal type is produced simply by an extension of the vascular system of the lemma into a long, pointed process known as the *awn*, or *beard*. The awns of most barleys are barbed from the base to the tip. This, however, does not hold for all varieties. A few cultivated varieties have smooth awns (fig. 61, B), and many more are being produced by hybridization. The smooth-awned

character seems to be of recent origin, as it was not described by the early writers on this subject. Recently Kornicke (1885), Regel (1906), and Harlan (1918) have described this condition as characteristic of some varieties. Professor F. P. Bussell, of the Department of Plant Breeding at Cornell University, has recently produced a smooth-awned type from a cross between two varieties with barbed awns. This character, whenever found, seems to be constant and is of considerable importance in distinguishing varieties, and is so used in the present classification. In certain varieties the awns are only sparingly barbed or are barbed only for a part of their length. Usually the upper third is barbed in such cases, while in other varieties, particularly in the dense-headed types, the barbing is very profuse. Thus, considerable variation is found in the degree of barbing. These lesser variations have little taxonomic value, as they are usually associated with more important characters. They have never been used in previous classifications. In the present classification they are used in varietal description.

A marked difference likewise occurs in both the deciduousness and the rigidity of the awns of different varieties. Some varieties, when mature, drop their awns very readily, and by threshing time the spikes are practically bare of awns. Most varieties, however, hold their awns very securely, some being broken off with difficulty even by threshing. This second condition is usually associated with a very rigid, coarse awn. These differences can be used only in varietal descriptions.

Some noticeable variations occur between varieties in the length and in the width of awns, but these are significant in varietal descriptions only when associated with other characters.

In the awnless type, as the term signifies, the lemma ends either in a point or bluntly. The awnless lemmas are always found on the sterile side spikelets of the two-rowed barleys, and occasionally on the fertile side spikelets of the six-rowed. The awnless type was described by Kornicke (1885), and has been used since in describing certain types and often in differentiating large groups and even species.

The third type of terminal appendage is found on what are known as *hooded barleys*. Here the normal awn is replaced by a trifurcate structure known as the *hood*. The morphological significance of this

appendage is not fully understood, but it seems that there is a partial repetition of the spikelets of a node, the three parts of the appendage representing the lemmas of the three spikelets. These glume-like structures frequently bear rudimentary sexual organs, but are seldom if ever fertile. The origin of this type is unknown, but it dates well back in cultivated barleys, since it was described by both Schübler (1818) and Séringe (1819). Since that time it has been used by all investigators along this line. The hooded condition usually appears on all fertile spikelets, but in certain six-rowed forms only the median spikelets are hooded. The only variation of importance in the hooded types is that found in the location of the hood. Commonly this structure is sessile, but in certain varieties it is elevated on an awn to a greater or less extent.

The three main types of barleys in regard to terminal appendage are of very great importance in the systematic grouping of cultivated barleys, both because of their constancy and because of the ease of determination. They are second only to fertility and adherence of the lemma and palea to the caryopsis, in the present classification.

Number of nerves of lemma

It is generally characteristic of the entire Hordeum genus to have five nerves in the lemma — one dorsal, and two lateral on either side, all of which are usually rather obscure. In cultivated varieties of barley, the number occasionally is increased from five to seven, and in some cases the nerves become very conspicuous. The latter variation is a matter of degree and can be used only in varietal descriptions. The increase in the number of nerves is, however, very definite and noticeable. For this reason it could be used in making more important divisions were it not for the fact that it occurs very infrequently.

Neither the variation in the number of nerves nor that in their prominence has been used in previous classifications for the purpose of forming main divisions or in describing varieties. In the present classification these variations are employed in order to separate certain varieties in the larger groups.

Barbing of lateral nerves of lemma

The variation in the character of the two lateral nerves next to the dorsal nerve was first pointed out by Neergaard (1889). After careful

study, he found that in certain varieties these nerves were toothed or barbed, while in other varieties they were perfectly smooth (fig. 62). This character proved to be constant and reliable. As a consequence it has been used widely in Sweden in recent years in differentiating certain varieties which were similar in all readily observable characters. Some workers following Neergaard, particularly Broili (1906), have held that this character was not constant, while others have supported Neergaard. As a consequence of this doubt as to the constancy of the character, it has not been used widely by recent investigators. In the present classification it is used to make rather important divisions of agricultural varieties, particularly of the two-rowed sorts.

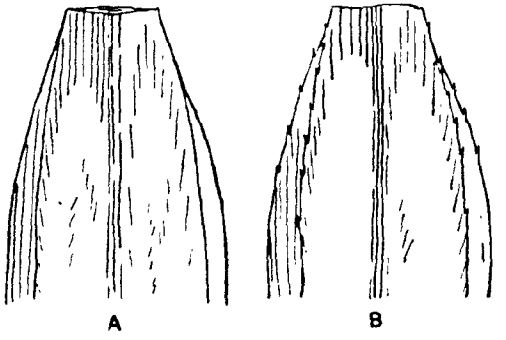


FIG. 62. VARIATION IN BARBING OF LATERAL NERVES OF LEMMA

A, Smooth lateral nerves; B, barbed lateral nerves

In employing this character, it is necessary in many cases to use a hand lens in order to be sure of the presence or the absence of the barbs. The character varies in a similar manner to the barbs on the awns. In some varieties the barbs extend along the lateral nerves nearly to the base of the kernel, while in other varieties there is a complete absence of barbs. Between these two conditions there are practically all degrees of barbing. This character, however, seems to be independent of the barbing of the awns, as some smooth-awned varieties have barbed lateral nerves and many varieties with barbed awns have smooth lateral nerves.

Base of lemma

The variation in the shape of the base of the lemma was first used to distinguish large groups of barleys by the Swedish investigators. They differentiated the erect compact forms from the nodding lax forms of two-rowed barleys by the character of the base. The first work on the Swedish system was begun by Atterberg (1889) and Bolin (1893). The narrow

lax forms of the two-rowed barleys are characterized by a slight horseshoe-shaped depression at the base on the dorsal side of the kernel (fig. 63, A and B). (As reported by Atterberg and Bolin, this difference was for hulled varieties only.) Associated closely with this character is the type of basilar connection of the kernel to the rhachis. The attachment is reduced to a narrow band of tissue, which separates at maturity leaving a smooth surface. Contrasted with these two characters of the narrow

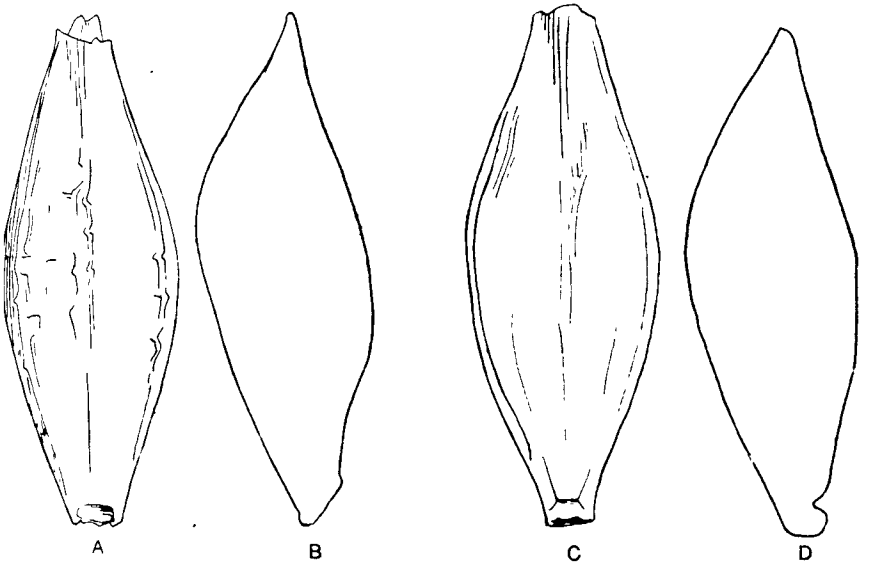


FIG. 63. VARIATION IN SHAPE OF LEMMA BASE

A, Dorsal view of lemma base of lax-headed barley, showing horseshoe-like depression; B, lateral view of same; C, dorsal view of lemma base of dense-headed barley, showing cross crease, D, lateral view of same

lax forms, the dense erect forms have a base which is often pinched in appearance, with a transverse crease or furrow just above the point of attachment but with no horseshoe-like depression (fig. 63, C and D). The basilar connection associated with this type of lemma is broader, and when separated leaves a rougher surface than does the basilar connection of the lax forms.

Although these characters have been used for differentiating only threshed two-rowed hulled types, they hold equally true for threshed six-

rowed hulled barleys and for hull-less types which are still in the spike. Their value in classification is somewhat limited because they are associated so closely with density.

The outer glumes

Each spikelet in barley, in common with practically all members of the grass family, is subtended by a pair of empty glumes, or bracts (fig. 60). These glumes in the case of barley are usually covered with fine hairs, are lanceolate in shape, and end either in awn points or in short awns. However, all three of these characters of the outer glumes vary.

Occasionally varieties appear with expanded outer glumes which are almost ovate in shape. This ovate shape appears in a few varieties on all six of the outer glumes, in others on the outermost two, and in rarer cases on the middle spikelet only. The shape of the outer glumes was first used by Körnicke (1885) for the separation of varieties, but was not considered of very great importance. More recently Beaven (1902) and Harlan (1918) have given it more weight as a taxonomic character. Another variation in shape of the outer glumes, which has not been previously described so far as the present writer knows, is in the terminal appendage. In very rare cases, hoods appear instead of awns on the two outermost outer glumes. This variation has been found in only one variety, and at present it has no value in classification.

Again, varietal differences occur in the length of awn on the outer glumes. This was first illustrated by Munro and Beaven (1900). In some cases the awns on the outer glumes are almost as long as the awns on the lemmas. This variation may occur on the outer glumes of the two lateral spikelets, on the median spikelets only, or in rare cases on all three spikelets of both the two-rowed and the six-rowed types.

The difference in hairiness of the outer glumes is only in degree. In many varieties the glumes are well covered with long, straight hairs, while in many others the hairs are much shorter and not nearly so abundant; in rare cases the glumes are practically glabrous. These variations, so far as observations have gone, are always associated with similar but more apparent characters of the rhachilla.

All the variations in the characters of the outer glumes are of minor importance in classification, either because they occur so rarely or because

they are closely associated with other structural characters. For these reasons they are used in the present classification only in varietal descriptions.

The rhachilla

The rhachilla, which is often known as the *basal bristle*, is the prolongation of the primary axis of the spikelet beyond the last floret — in the case of barley the only floret. The entire structure of a barley spikelet is shown diagrammatically in figure 60. In perfectly sessile barleys the rhachilla is the only evidence of the primary axis of the spikelet. It is more or less hidden in the groove on the ventral side of the kernel, remaining undisturbed in the case of hulled barleys when the grain is threshed. The rhachilla presents one pair of differentiating characters which is of very great taxonomic value. In one group of varieties the rhachilla is short and is abundantly covered with long, straight, hairs; while in another group it is almost twice as long and is covered sparingly with short, curly hairs, giving a woolly appearance to the whole structure. This difference is illustrated in figure 64.

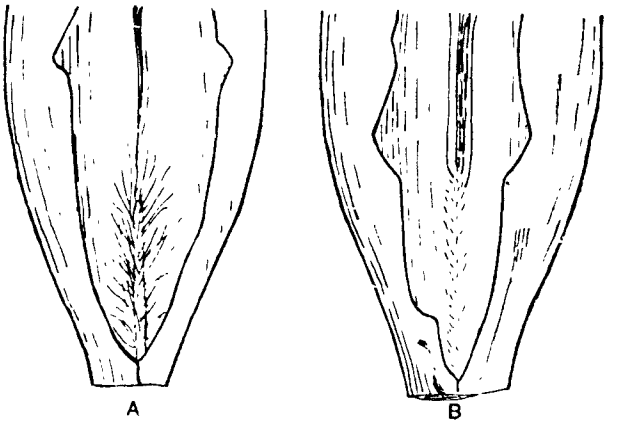


FIG. 61. THE RHACHILLA

A, Long-haired rhachilla; B, short-haired rhachilla

This pair of characters, like the variation in the character of the barbing on the lateral nerves, was discovered by the Swedish investigators. They have found the variation in the rhachilla even more reliable and of greater value than the variation in the barbing of the lateral nerves, in the identification of barley varieties grown in Sweden. In the present classification this pair of characters is employed in the separation of the lesser groups of varieties.

Occasionally another variation occurs in the rhachilla, in that a rudimentary second floret is produced. This variation has been used occasionally in describing varieties, but, so far as the observations made in the present study go, it is of little or no value. It seems to be the result of either a sterile first floret or poor adaptation. Whenever it appears it is usually in connection with poorly developed heads, not as a characteristic of any variety or group of varieties.

SUMMARY

In order to eliminate possible confusion in regard to the characters used in the present classification and to gain some idea of their relative importance, the following brief summary of their use herein is given:

To distinguish species and subspecies:
1. Articulation of rhachis
2. Fertility of lateral spikelets
3. Presence of sexual organs in side spikelets
4. Presence of terminal appendages on lemmas of side spikelets

To distinguish the several varieties within large groups:
1. Adherence of lemma and palea to caryopsis
2. Variations in terminal appendage
3. Color
4. Density of spike as determined by
   a. Base of lemma, or flowering glume
   b. Length of rhachis internode
   c. Width of spike
5. Character of rhachilla
6. Presence or absence of barbs on awns
7. Habit of early growth
8. Presence or absence of barbs on lateral nerves of lemma

To distinguish the subvarieties or strains within the more important varieties:
1. Attitude of spike
2. Date of emergence of awns and spikes
3. Time of maturity
4. Outer glumes
5. Grain characters:
   a. Composition
   b. Size
   c. Shape
6. Variations in size and color of foliage
7. Culm characters:
   a. Length of last internode
   b. Total length of culm
   c. Number of nodes
8. Variation in articulate character of rhachis
9. Branch-headed character
10. Productivity

Many of the last-named characters are influenced to such a degree by environment that they cannot be used alone to make differentiations,

but when combined with other characters they may be employed in separating subvarieties. These characters are more valuable in varietal description than for any other purpose, and can be employed only for local identification.

CLASSIFICATION OF BARLEY FORMS

The classification as given in the following pages is very largely of cultivated varieties, this being the main purpose of the study. Some unimportant varieties are included, however, in order to make the classification more nearly complete. It has likewise been considered better to construct the keys to groups and varieties in such a way that they may easily be expanded to include new introductions and new productions which are certain to arise. For this reason, and because of a lack of specimens possessing all the possible combinations of characters, the keys are left incomplete, some divisions failing to appear in certain instances.

The cultivated species of barley (fig. 65), and the one wild species (*Hordeum spontaneum*, fig. 58) which is most closely related, may be distinguished according to the following key:

		PAGE
A. Rhachis articulate	*Hordeum spontaneum.*	415
AA. Rhachis non-articulate.		
B. All spikelets fertile.		
C. Lemmas of all spikelets awned or hooded, kernels of all spikelets equal or nearly equal in size	*H. vulgare.*	416
CC. Lemmas of central spikelets awned or hooded, lemmas of lateral spikelets bearing neither awns nor hoods, kernels of lateral spikelets much reduced in size	(x) *H. intermedium*[1].	430
BB. Only the central spikelets fertile.		
C. Lateral spikelets possessing nonfunctional rudimentary sexual organs. . .	*H. distichon.*	433
CC. Lateral spikelets much reduced in structural parts and possessing no rudimentary sexual organs.	*H. deficiens.*	443

The general relationship of the species may be graphically shown as follows:

Family	Genus	Species
Gramineae	Hordeum	*spontaneum* *vulgare* (x) *intermedium* *distichon* *deficiens*

[1] The x before *H. intermedium* indicates the hybrid origin of this species, also that it is not of equal rank with the other species.

FIG. 65. FOUR CULTIVATED SPECIES OF BARLEY

A, *Hordeum deficiens*; B, *H. distichon*; C, *H. intermedium*; D, *H. vulgare*

In the present classification the number of species of cultivated varieties is placed at four, one of which, *H. deficiens*, is at present of lesser agronomic importance than the others. These groups are given the species distinction largely because (1) all the best evidence seems to point to the very early origin and to the parallel development of these types; (2) the numerous distinct varieties are less confusing when placed in four rather than in one species; (3) most of the earlier investigators have used more than one species. It is evident, however, that these species are not so distinct as are many species of other plants, especially in the wild state, since in many cases interspecies crosses are impossible. In barley, the species as designated in the present classification readily cross.

HORDEUM SPONTANEUM

Hordeum spontaneum C. Koch (fig. 58) differs from all the cultivated forms of barley by the articulation of the rhachis. At or near maturity the rhachis separates at each node but the segments remain attached at the upper end to the spikelets. The rhachises of cultivated barleys, on the other hand, do not readily disarticulate at maturity. If the spikelets are forced apart, they break loose from the rhachis and leave it entire. It seems that in the evolution of cultivated barleys the rhachis has become solidified into a single structure.

The character of the brittle rhachis is found in several wild grasses, among the most interesting of which is the wild wheat of Palestine, the possible progenitor of cultivated wheats. This characteristic makes these grasses especially adapted for reseeding, and may account for the continued existence of these forms in nature.

H. spontaneum has been known to botanists for many years, having been described by Post (1883), by Boissier (1884), and by Hochstetter (1848). By both Boissier and Post it was designated as *Hordeum Ithaburense*. It may be briefly described as follows:

Leaves weak, linear, tapering at tip; spikes awned, flattened, two-ranked; rhachis brittle, plumose; lateral spikelets pointed, without awns, staminate, pedicillate; central spikelet awned, perfect, sessile, awns very long and excessively barbed; dorsal nerves of flowering glumes of lateral spikelets smooth; outer glumes of all spikelets very hairy, awned; awns 1½ times as long as lateral florets; rhachilla long, covered with long, straight hairs; kernel long, slender.

The only interest in this type from an economic standpoint lies in the possibility of its being the ancestor of some if not all of the cultivated barleys.

HORDEUM VULGARE

Hordeum vulgare L. (figs. 66 and 67), one large species of cultivated barleys, is differentiated from the wild species just described principally

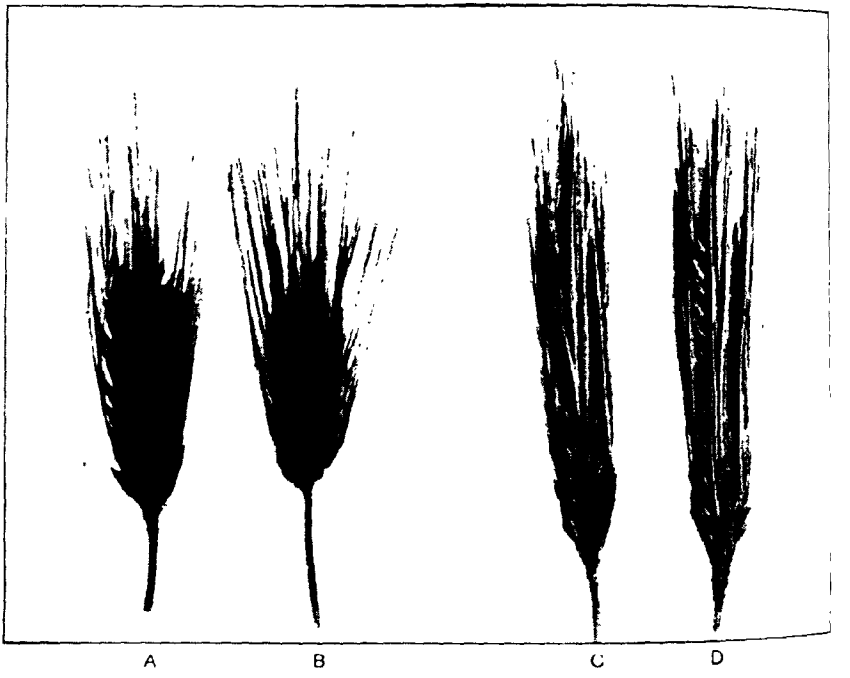


FIG. 66. VARIETIES OF HORDEUM VULGARE

A and B, Dense hulled forms; C, lax hulled; D, lax hull-less

by the presence of a solidified rhachis, one which holds together at maturity and remains intact even though the kernels are broken off. Another important difference between the two is found in the fertility of the spikelets. In *H. vulgare* all three spikelets at each node of the rhachis are fertile, thus forming six rows of fertile spikelets instead of two. The species may be briefly described as follows:

Spike erect and nodding, six- or four-ranked according to arrangement of spikelets: rhachis, or central axis of spike, made up of a number of short internodes which are solidified at the joints; spikelets arranged in groups of three at each joint in the rhachis, all equally fertile, all awned or hooded, all sessile or nearly so, awns usually barbed; lateral nerves of flowering glumes barbed or smooth; rhachilla hairy; grains of lateral

FIG. 67. VARIETIES OF HORDEUM VULGARE
A, Lax, hulled, awned; B, lax, hulled, hooded; C, lax, hull-less, awned; D, lax, hull-less, hooded

spikelets equal or nearly equal in size to grains of central spikelets; grains varying in size and shape from long and slender to short and plump; grains either hulled or hull-less.

H. vulgare includes practically all the important cultivated varieties of the six-rowed barleys. It is more important in the United States than any other species, although both *intermedium* and *distichon* are grown

rather extensively. Varieties of the *vulgare* type are found to do best in Minnesota, Wisconsin, Illinois, Iowa, and Nebraska. The culture of this species is by no means limited to the United States; it is grown wherever barley is cultivated to any extent, and in European countries it ranks second only to *distichon*.

Key to varieties of H. vulgare[8]

A. Kernels hulled. PAGE
B. Lemmas awned.
C. Kernels white, blue, or purple.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.5 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
H. Lateral rows of spikelets overlapping more at tip than at base of spike; kernels medium to small in size, under 1 cm. in length; heads nodding; awns showing tendency toward deciduousness.
I. No pigment in aleurone layer, white or yellow
Manchuria Selection 29
II. Pigment present in aleurone layer, blue Featherston 41
HH. Lateral rows of spikelets overlapping the same from base to tip of spike; kernels long and coarse, usually 1 cm. or more in length; straw coarse and short under New York environment; awns stiff and harsh, having no tendency toward deciduousness.
II. Pigment present in aleurone layer, blue Morocan 41
GG. Winter habit of early growth.
H. Lateral rows of spikelets overlapping more at tip than at base of spike; kernels medium to small in size, under 1 cm. in length; heads nodding; awns showing tendency toward deciduousness.
II. Pigment present in aleurone layer, blue
Mammoth Winter 42
EE. Rhachilla beset with short, fine hairs.
F. Awns barbed.
G. Spring habit of early growth.
H. Lateral rows of spikelets overlapping more at tip than at base of spike; kernels medium to small in size, under 1 cm. in length; heads nodding; awns showing tendency toward deciduousness.
I. No pigment in aleurone layer, white or yellow
Manchuria-Odessa Hooker 42
II. Pigment present in aleurone layer, blue O. A. C. 21 43

[8] The naming of all groups and varieties conforms to the rules of varietal nomenclature adopted by the American Society of Agronomy at its annual meeting held November 12–13, 1917, and published in the Journal of the society, volume 9, no. 9, 1917, with the exception of the cases in which the [illegible] of both these given by the Office of Foreign Seed and Plant Introduction, United States Department of Agriculture, S. P. I., and the selection numbers employed by the author. It is considered [illegible] numbers to denote specimens with a given group of characters until a variety of commercial importance with the same characters is found, rather than to fix permanent names to the already existing [illegible] specimens. Appropriate varietal names may be readily fixed at any later date.

PAGE

HH. Lateral rows of spikelets overlapping the same from base to tip of spike; kernels long and coarse, usually 1 cm. in length; straw coarse and short under New York environment awns stiff and harsh, having no tendency toward deciduousness.
I. No pigment in aleurone layer, white or yellow. Mariout. 423
II. Pigment present in aleurone layer, blue . Bay Brewing. 424
GG. Winter habit of early growth.
H. Lateral rows of spikelets overlapping more at tip than at base of spike; kernels medium to small in size, under 1 cm. in length; heads nodding; awns showing tendency toward deciduousness.
I. No pigment in aleurone layer, white or yellow . Idaho Winter. 425
II. Pigment present in aleurone layer, blue . . German Winter. 425
DD. Spikes broad, dense, erect; internodes of rhachis short (1.5–2.8 cm. to ten internodes); base of lemma cross-creased.
E Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
H. Outermost glumes of side spikelets very broad.
I. No pigment in aleurone layer, white or yellow . Triumph. 425
HH. All outer glumes the same size.
I. No pigment in aleurone layer, white or yellow; side spikelets sessile Utah Winter. 425
II. Pigment present in aleurone layer, light blue; foliage dark green S. P. I. 41159. 426
GG. Winter habit of early growth.
H Density 2.5 cm. or less to ten internodes of rhachis.
I. No pigment in aleurone layer, white or yellow Short Six-rowed Winter. 426
EE. Rhachilla beset with short, fine hairs.
F Awns barbed.
G. Spring habit of early growth.
H. Density 2.5 cm. or less to ten internodes of rhachis.
I. No pigment in aleurone layer, white or yellow . Chilian. 426
CC. Kernels black.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.5 cm. to ten internodes), base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth . . . Gatami. 426
GG. Winter habit of early growth . . . . Black Winter. 426
FF. Awns smooth.
G. Spring habit of early growth . Black Summer. 426
BB. Lemmas hooded.
C. Kernels white, blue, or purple.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.5 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with short, straight hairs.
F. Spring habit of early growth.
G. No pigment in aleurone layer, white or yellow . . . . . Success. 427

PAGE

DD. Spike broad, dense, erect; internodes of rhachis short (1.5–2.8 cm. to ten internodes[1]); base of lemma cross-creased.
E. Rhachilla beset with long, straight hairs.
F. Spring habit of early growth.
G. No pigment present in aleurone layer, white or yellow
Selection 250, 427

AA. Kernels hull-less.
B. Lemmas awned.
C. Kernels white, blue, or purple.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.5 cm. to ten internodes[1]); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
H. No pigment in aleurone layer, white or yellow.
I. Lateral nerves smooth — Cockette 427
II. Lateral nerves barbed — Hansen Hulless 427
HH. Pigment present only in aleurone layer, blue
Guy Mayle 428
HHH. Pigment present in aleurone and pericarp layers, purple
Black Hulless 428
EE. Rhachilla beset with short, fine hairs.
F. Awns barbed.
G. Spring habit of early growth.
H. No pigment in aleurone layer, white or yellow.
I. Awns 10 cm. or more in length — Utah Hulless 428
II. Awns 5 cm. or less in length — S. P. I. 41156 429
DD. Spike broad, dense, erect, internodes of rhachis short (1.5–2.8 cm. to ten internodes[1]); base of lemma cross-creased.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of growth.
HH. Pigment present in aleurone layer, blue . S. P. I. 41157 429
BB. Lemmas hooded.
C. Kernels white, blue, or purple.
D. Spike narrow, lax, nodding, internodes of rhachis long (3.0–4.5 cm. to ten internodes[1]); base of lemma with horseshoe-like depression
E. Rhachillas beset with long, straight hairs.
F. Spring habit of growth.
G. No pigment present in aleurone layer, white or yellow
White Hulless 429
CC. Kernels black.
DD. Spike narrow, lax, nodding; internodes of rhachis short (1.5–2.8 cm. to ten internodes[1]), base of lemma with horseshoe-like depression
E. Rhachillas beset with long, straight hairs.
F. Spring habit of growth . . . Selection 308, 430

Descriptions of varieties

Manchuria Selection.—Foliage medium green; culms strong, average in size and length; erect in early habit of growth; spikes well out of

[1] Selection numbers as used in this and the following keys are either applied to selections made from mixed specimens or to unnamed specimens which are of no commercial value at present

ast leaf sheath at maturity; medium to early in maturity; length of ten nternodes of rhachis, 3.0–4.5 cm.; spikes nodding; angle of inclination f kernel with rhachis, small; lateral rows of spikelets overlapping more t tip than at base of spike; grain short and usually plump, white or ellow in color, hulled, awned; awns showing only slight tendency toward leciduousness; lemma barbed, base with horseshoe-like depression; hachilla beset with long, straight hairs.

The following key separates the subvarieties of the variety Manchuria Selection:

A. Early in maturity; awns medium strong, with slight tendency toward deciduousness; spikes usually nodding more than 90°, straw strong.
  B. Rhachis solidified — Manchuria Selection.
    (Additional specimens found under the following names: Australian Early, Bernards, Black Two-rowed, Ouchac.)
BB. Rhachis somewhat brittle when kernels are broken apart.
  C. Foliage medium green — Norwegian I.
    (An additional specimen found under the name Norwegian Bjorneleyg.)
  CC. Foliage light green — Australian Early.
AA. Medium in maturity; awns weak, with strong tendency toward deciduousness; spikes usually nodding less than 90° — French Early.
  (Additional specimens found under the following names: French Gerste aus Denmark, Long-grained Winter.)

Featherston — The variety Featherston is distinguished from Manchuria Selection by possessing light pigment in the aleurone layer, which gives a light blue color to the kernels. Otherwise the two varieties are very similar.

The following key separates the subvarieties of the variety Featherston:

A. Very early in maturity; culms very short; spike and awns short — S. P. I. 18922.
AA. Medium to early in maturity, culms, spikes, and awns medium in length.
  B. Spikes erect or nearly erect; culms long — Australian Winter.
BB. Spikes nodding; culms medium in length.
  C. Spikes long and very nodding; rhachis solidified — Featherston.
  CC. Spikes medium in length and slightly nodding; rhachis slightly brittle — Gerste aus Morocco.
    (An additional specimen found under the name Mezoeijes Handgerste aus Ungarn.)

Moroccan.— Foliage medium green; culms coarse and short under ew York conditions; erect in early habit of growth; spikes well out sheath of last leaf at maturity; medium to early in maturity; spikes x, length of ten internodes of rhachis 3.0–4.5 cm.; angle of inclination kernel with rhachis, small; lateral rows of spikelets overlapping the me from tip to base; grain long and coarse, over 1 cm. in length, light ue in color, hulled, awned; awns stiff and harsh, having no tendency

toward deciduousness; lemma barbed, base showing horseshoe-like depression; rhachilla beset with long, straight hairs; very poorly adapted to New York environment.

The following key separates the subvarieties of the variety Moroccan:

A. Very early in maturity; culms and spikes very short.
  B. Heads erect or inclining only slightly.
    C. Density of spike less than 3.4 cm. to ten internodes of rhachis — Marvar
      (Additional specimens found under the following names: S. P. I. 41160, S. P. I. 41161, S. P. I. 41158.)
    CC. Density of spike more than 3.4 cm. to ten internodes of rhachis — Guzerat
      (Additional specimens found under the following names: Australian Imperial, India Cawnpur, India Punjake, Indian Sind.)
  BB. Heads nodding.
    C. Outer glumes short-awned, total length of awn and glume two to three times that of lemma — Cawnpur
    CC. Outer glumes awn-pointed, total length of awn and glumes scarcely more than length of lemma — Grado
      (Additional specimens found under the following names: Beldi, Canary Island, Tripolitan.)
AA. Medium in maturity; culms and spikes medium to short.
  B. Outer glumes short-awned, total length of awn and glume more than twice that of lemma — Marvar
    (An additional specimen found under the name Manchuria.)
  BB. Outer glumes awn-pointed, total length of awn and glume scarcely more than length of lemma — Moroccan
    (Additional specimens found under the following names: Algeria, German Hanna, Spanish Sierra Yqua, Tunisian.)

Mammoth Winter.— Foliage medium green; culms medium to long; winter habit of early growth; early-maturing when compared with spring barleys; spike nodding and lax, 2.8–4.0 cm. to ten internodes; lateral rows of spikelets overlapping almost completely at tip of spike; kernels slightly pigmented, medium in size, plump; lemma awned, horseshoe-shaped at base; outer glumes extending slightly beyond kernel; rhachilla beset with long, straight hairs.

Additional specimens were found under the following names: Eckendorfer Mammoth Wintergerste, Friedrichswerther Mammoth Wintergerste, Klein Wanzlebener Wintergerste, Wustermarsch Wintergerste.

Manchuria-Oderbrucker (Plate XXXIV, 1).— The variety Manchuria-Oderbrucker is distinguished from Manchuria Selection by the character of the rhachilla, which is beset with short, fine hairs more or less recurved at the tip, thus presenting a woolly appearance. Also, the rhachilla is usually from 30 to 60 per cent longer. This variety presents more sub-varieties than does Manchuria Selection, as is seen by the accompanying

ey. Manchuria-Oderbrucker is by far the most important variety of arleys in the United States. It is the leading variety in the large arley-growing section comprising Minnesota, Wisconsin, Nebraska, Iowa, nd Illinois.

The following key separates the subvarieties of the variety Manchuria-)derbrucker:

A. Outer glumes awn-pointed, scarcely extending beyond lemma — Odessa.
A Outer glumes short-awned, extending to two or more times the length of lemma.
B. Lateral nerves not barbed; awns deciduous or nearly so; foliage light green. . . . Gerste aus Norwegen.
BB. Lateral nerves barbed; awns slightly deciduous; foliage medium green.
C Early in maturity; culms short — Norwegian II.
(Additional specimens found under the following names: French Early, Norwegian Bamsleyg, Norwegian Bjorneleyg.)
CC. Medium in maturity and in length of culms. . . Manchuria-Oderbrucker.
(Additional specimens found under the following names: Australian Winter, California Portuguese, Canada, Canadian Fancy, Eagle, Featherston Selections, French Early, Gerste aus Ajaccio, Gerste aus Lulea, Idaho Callow, Kleine Warthebruch, Manchuria, Manchurian, Manchuria Selections, Manchury, Minnesota 6, Oderbrucker, Red River, Red's Triumph, Rumanian Autumn, Schlesische Zeilgerste, Siberian, Swedish Six-rowed, Swiss Spring, Turkish Albanian, Wisconsin 5, Wisconsin 6, Wisconsin Pedigree.)
CCC. Late in maturity; medum to long culms . . Roumanian Spring.
(Additional specimens found under the following names: Heavy Moldavian, Odessa, Roumanian Autumn, Silver King.)

O. A. C. 21 (Plate XXXIV, 2). — The variety O. A. C. 21 differs from lanchuria-Oderbrucker only by possessing pigment in the aleurone layer, hich gives the grain a light blue color. Some variation exists between ie subvarieties within this variety, as is shown by the following key:

A. Lateral nerves smooth or with very few barbs.
B. Awns with strong tendency toward deciduousness . South African Cape Early.
(An additional specimen found under the name Russian Livonian.)
BB. Awns without tendency toward deciduousness . Gerste aus der Mandschursi.
(An additional specimen found under the name Manchury.)
A Lateral nerves barbed.
B. Early in maturity — S. P. I. 40648.
(An additional specimen found under the name S. P. I. 40649.)
BB. Medium in maturity . — O. A. C. 21.
(Additional specimens found under the following names: Blue Ribbon, Brachyura kurze Sechszeilige Gerste, Canada, Canadian 21, Canadian Western, Common, Featherston 507, Gerste aus Dalekartuen, Gerste aus Japan, Hemes Vierzeilige Gerste, Imp. Manchuria, Indian Sind, Oderbrucker, Odessa, Silver King, South Russian, S. P. I. 40645.)
BB Late in maturity . . . — South Russian.
(An additional specimen found under the name Gerste aus Cypern.)

Manchuria – Foliage dark green; culms short and small; erect in early owth, early in maturity; spike erect or nearly so, rather dense; grain

large and long, without pigment; lemma awned; awns very stiff and harsh; five nerves of lemma conspicuous, lateral nerves barbed; base of lemma with horseshoe-like depression; outer glumes short, narrow, awn-pointed; rhachilla sparingly beset with rather short, straight hairs.

The following key separates the subvarieties of the variety Mariout:

A. Outer glumes short, awn-pointed, scarcely extending beyond lemma; length of ten internodes 2.9–3.1 cm.; awns very stiff and harsh ..... Mariout.
AA. Outer glumes short-awned, length of awn and glume more than twice that of lemma; length of ten internodes 3.4–3.9 cm.
B. Medium in maturity ..... Yerli.
(Additional specimens found under the following names: Sandrel, Smyrna, Smyrna Yerli, Turkish (Rhodes to Sea of Marmora), Turkish Alasheir, Wisconsin Winter.)
BB. Late in maturity ..... C. I. 519.

Bay Brewing (Plate XXXIV, 3).— Foliage varying from light to dark green in different subvarieties; culms rather coarse and short in New York environment; erect in early growth; heads fully emerged at maturity from sheath of last leaf; medium to late in maturity; spike lax but not nodding as much as in Manchuria-Oderbrueker; lateral rows of spikelets overlapping the same from base to tip of spike; grain long and coarse, usually over 1 cm. in length; pigment in aleurone layer; grain hulled, awned, awns stiff, harsh, barbed, usually having no tendency toward deciduousness; nerves of lemma barbed; base of lemma with horseshoe-like depression; rhachilla beset with short, fine hairs, usually more or less recurved at tip.

This variety is second among all the varieties of *H. vulgare* in economic importance, although it is not adapted to New York conditions. It is particularly well adapted to the Pacific Coast States, where it is grown extensively.

The following key separates the subvarieties of the variety Bay Brewing:

A. Foliage medium to dark green; medium to late in maturity; leaves medium in length and width; erect in early growth.
B. Outer glumes awn-pointed, length of awn and glume about the same as lemma ..... Bay Brewing.
C. Medium in maturity ..... Chilean Brewing.
(Additional specimens found under the following names: Australian Loosdorfer (Early), Austrian, Algerian, Beldi, Blue Virginia, California, California (Early), Moravian, California Portuguese, California Prolific, Chili, Corcoran, Guatemalan Tontonicipan, Maltese Island, Moroccan, Orchac, Peru, Poda, South African Cape Early, South African Six-rowed, Swiss, Tunisian
CC. Late in maturity ..... Prosowetz, Cape.
(Additional specimens found under the following names: Australian, Australian Prosowetz, Cape.)

BB. Outer glumes short-awned, length of awn and glume two or more times length of lemma . . . . . Telli.
(Additional specimens found under the following names: Featherston, Grecian *Hordeum* sp., Montana, Tenkan, Turkish Smyrna Lowland.)

AA. Foliage light green; very late in maturity; leaves long and very broad, giving a leafy appearance; somewhat spreading in early growth.
B. Strong tendency toward brittle rhachis . . . . . Netherlans.
BB. Solidified rhachis. . . . . Swiss.

Idaho Winter.— Characterized by winter habit of early growth, early maturity, short-haired rhachilla, barbed awns, rather long spikes, lateral ows of spikelets overlapping almost completely at tip of spike, and onpigmented grain.

The following key separates the subvarieties of the variety Idaho Winter:

A. Outer glumes awn-pointed, length of awn and glume from one to two times that of lemma.
B. Foliage medium green; outer glumes extending beyond lemma . . Groninger.
BB. Foliage light green; outer glumes about same length as lemma . . Idaho Winter.
A. Outer glumes short-awned, total length of awn and glume about three times that of lemma . . . . . Alashier.

German Winter.— Distinguished from Idaho Winter by having kernels ith pigment in the aleurone; otherwise the same.

Triumph.— Foliage light green; culms medium to long; erect in early owth; late in maturity; average density 2.4–2.6 cm. to ten internodes; ikes long, somewhat nodding; grain nonpigmented, short; lemma rved; awns barbed, showing strong tendency toward deciduousness; rves of lemma barbed; base of lemma showing cross crease; lateral ikelets somewhat pedicellate; two outer glumes of side spikelets farthest om median spikelet very broad, about one-half width of lemma; rhachilla set with long, straight hairs.

Utah Winter (Plate XXXIV, 4).— Distinguished from Triumph by ving all outer glumes the same size, darker green foliage, shorter, denser ikes (average density 1.8–2.2 cm. to ten internodes), earlier maturity, ndeciduous awns, and sessile side spikelets. Representatives of the tah Winter variety do not behave as do winter barleys in New York vironment.

The following key separates the subvarieties of the variety Utah nter:

A. Foliage very dark green; late in maturity; outer glumes narrow and short-awned, total length of awn and outer glume about twice that of lemma; awns nearly parallel . Utah Winter.
(An additional specimen found under the name Californian.)

AA. Foliage medium green; medium to early in maturity; outer glumes broad and short-awned, total length of awn and outer glume about three times that of lemma; awns spreading.
B. Very early in maturity; culms short . . . . . Ogara
BB. Early to medium in maturity; culms very short . . . . . Hitakawa
(An additional specimen found under the name Chilian.)

S. P. I. 41159.— Distinguished from Utah Winter by having a pigmented aleurone layer and pedicellate side spikelets.

Short Six-rowed Winter (Plate XXXIV, 5).— Foliage medium green; culms medium to long; winter habit of growth; early in maturity when seeded in fall, but very late when seeded in spring; spike dense, 2.2 cm. to ten internodes, and erect; angle of inclination of grain with rhachis large; grain rather large and somewhat coarse; lemma thick, awned, cross-creased at base; awns barbed, spreading, rather stiff; rhachilla beset with long, straight hairs.

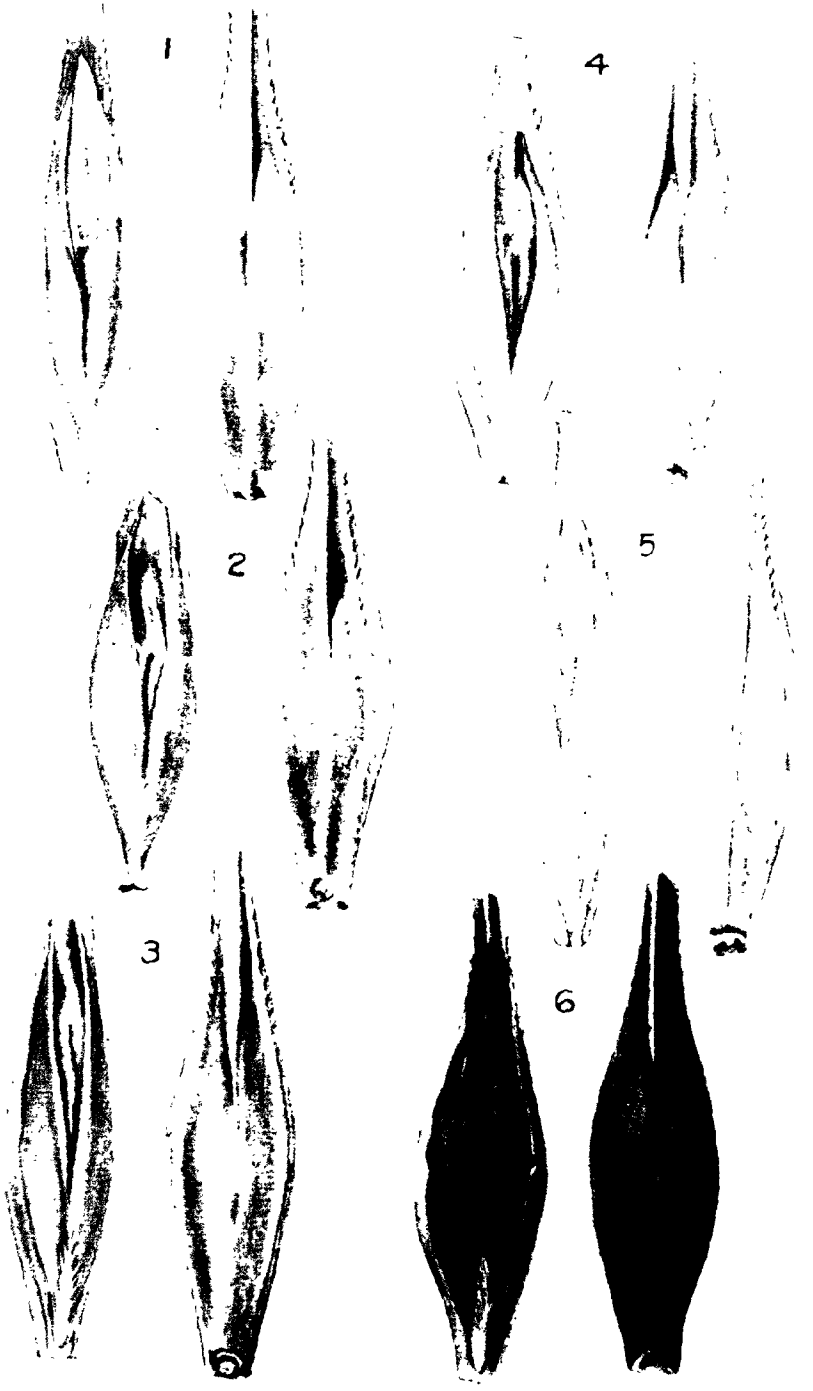
Chilian.— Distinguished from Utah Winter by having grain with a pigmented aleurone layer, and short, fine-haired rhachilla.

An additional specimen was found under the name Japanese Hitakawa.

Gatami (Plate XXXIV, 6).— Foliage light green; culms medium to short, fine, rather weak; erect in early growth; spikes well out of sheath of last leaf at maturity; medium in maturity; spikes lax, 3.4–3.6 cm. to ten internodes, nodding; grain small, dark gray in color, black pigment sometimes absent from base of lemma; lemma adhering closely to caryopsis, awned; awns barbed, medium to long, stiff; five nerves of lemma conspicuous; lateral nerves barbed; base of lemma with horseshoe-like depression; outer glumes narrow, awn-pointed; rhachilla beset with long, straight hairs.

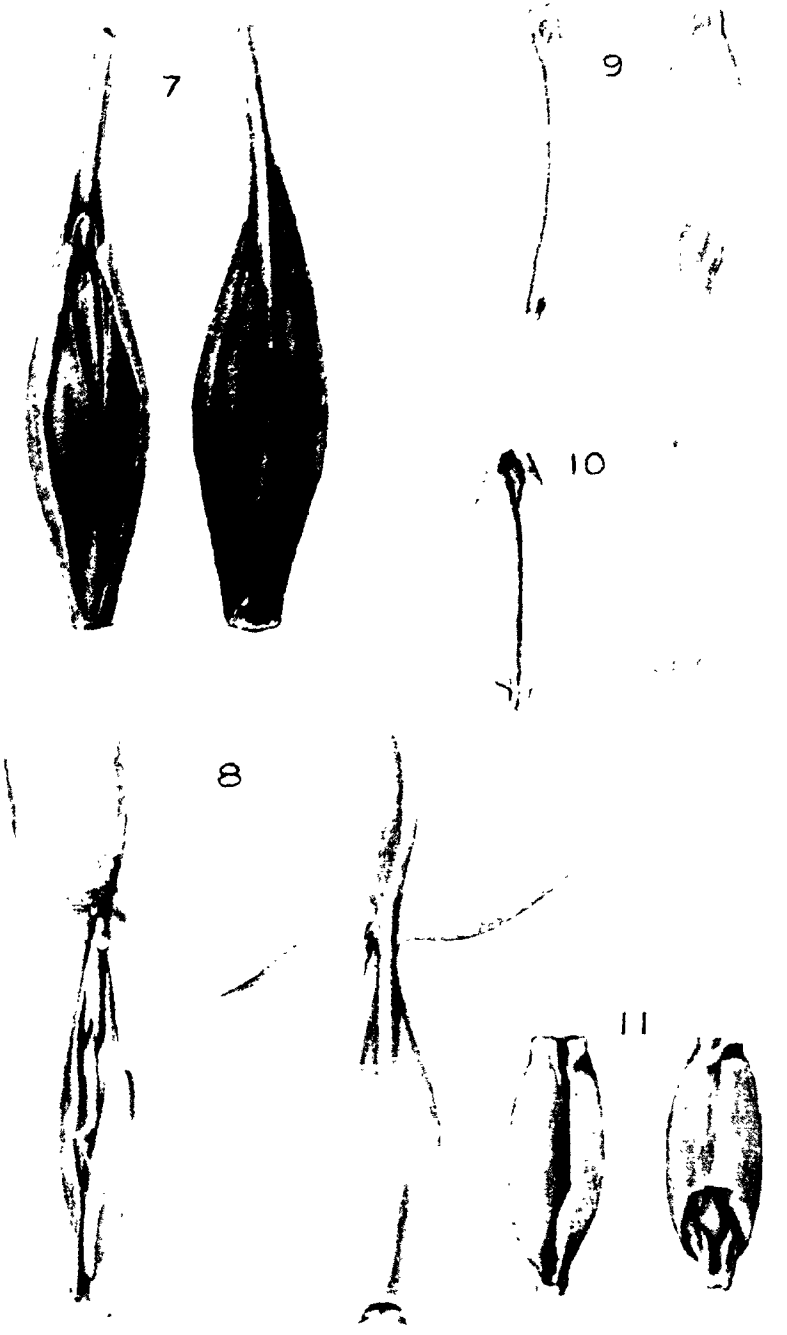
Black Winter.— Foliage medium green; culms long, strong; winter habit of early growth, scarcely maturing any seed when sown in the spring; early in maturity when fall-sown but late when spring-sown; spikes lax, 3.5–3.8 cm. to ten internodes, nodding, very long; rows of side spikelets overlapping almost completely at tip of spike; grain long, black, more or less glaucous; lemma adhering closely to caryopsis; five nerves of lemma scarcely distinguishable; lateral nerves barbed; base of kernel with horseshoe-like depression; outer glumes narrow, awn-pointed; rhachilla beset with long, straight hairs.

Black Summer (Plate XXXV, 7).— Foliage light green; culms medium to short, fine, rather weak; spikes well out of sheath of last leaf at maturity; medium to late in maturity; spikes lax, 3.4–3.6 cm. to ten



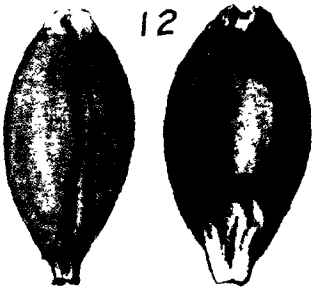
VARIETIES OF HORDEUM VULGARE

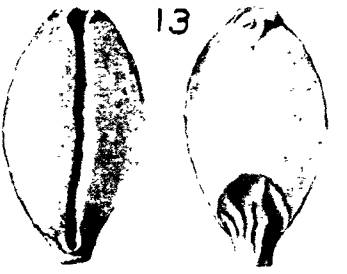
1, Manchuria-Oderbrucker; 2, O. A. C. 21, 3, Bay Brewing, 4, Utah Winter, 5, Short Six-rowed Winter, 6, Gatami

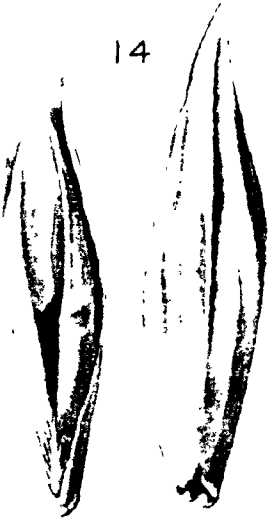


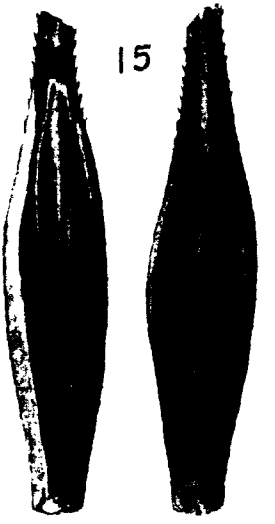
VARIETIES OF HORDEUM VULGARE

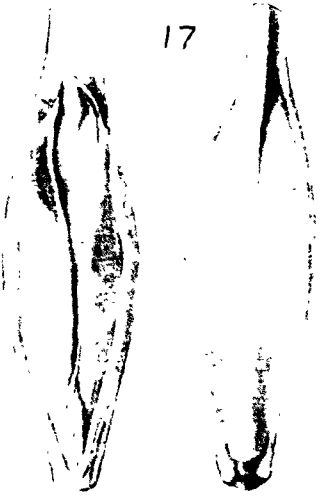
7, Prize Winner 8, Success, 9, Coolgrain, 10, Hansee Hulless 11, Guy Mayle





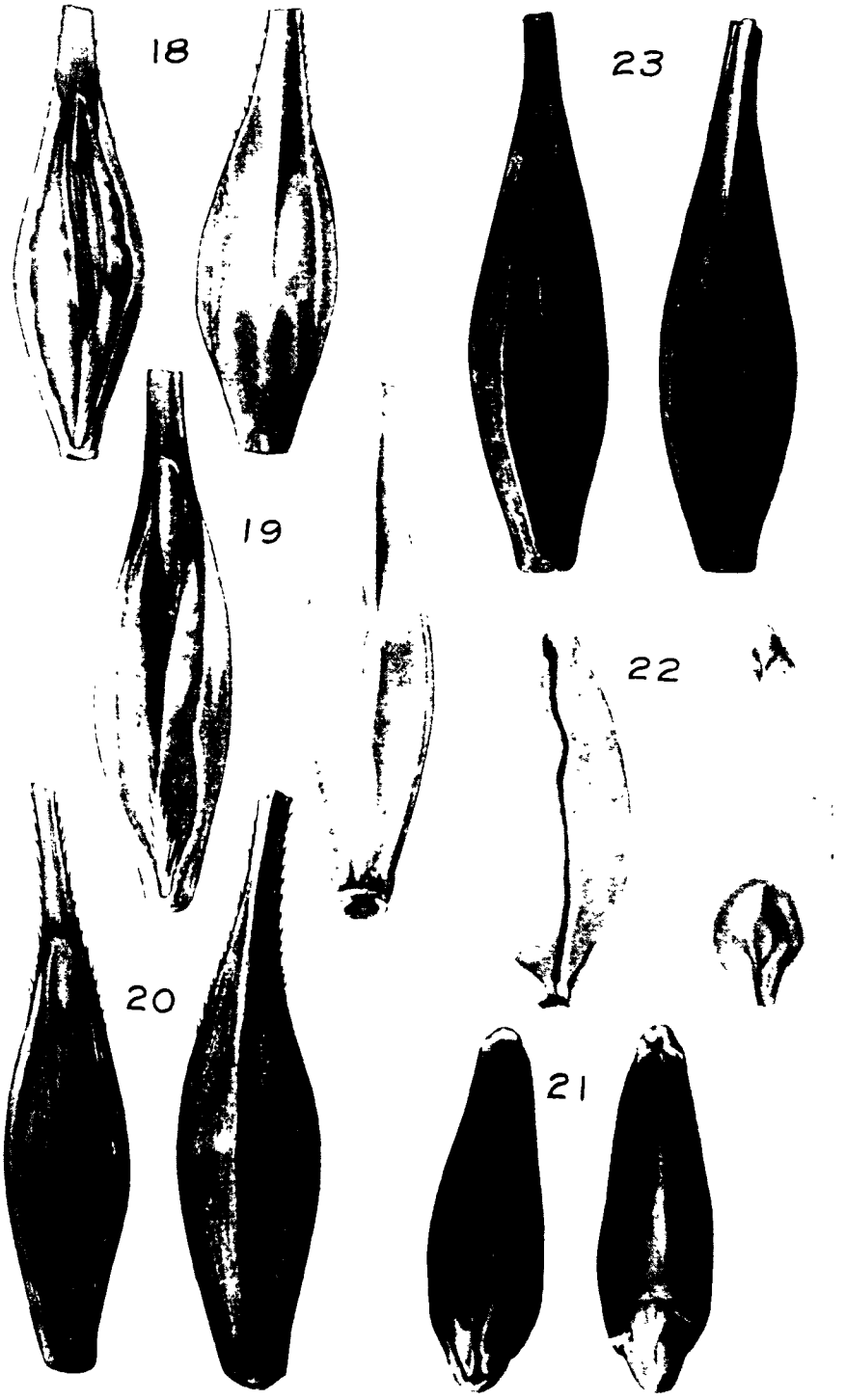






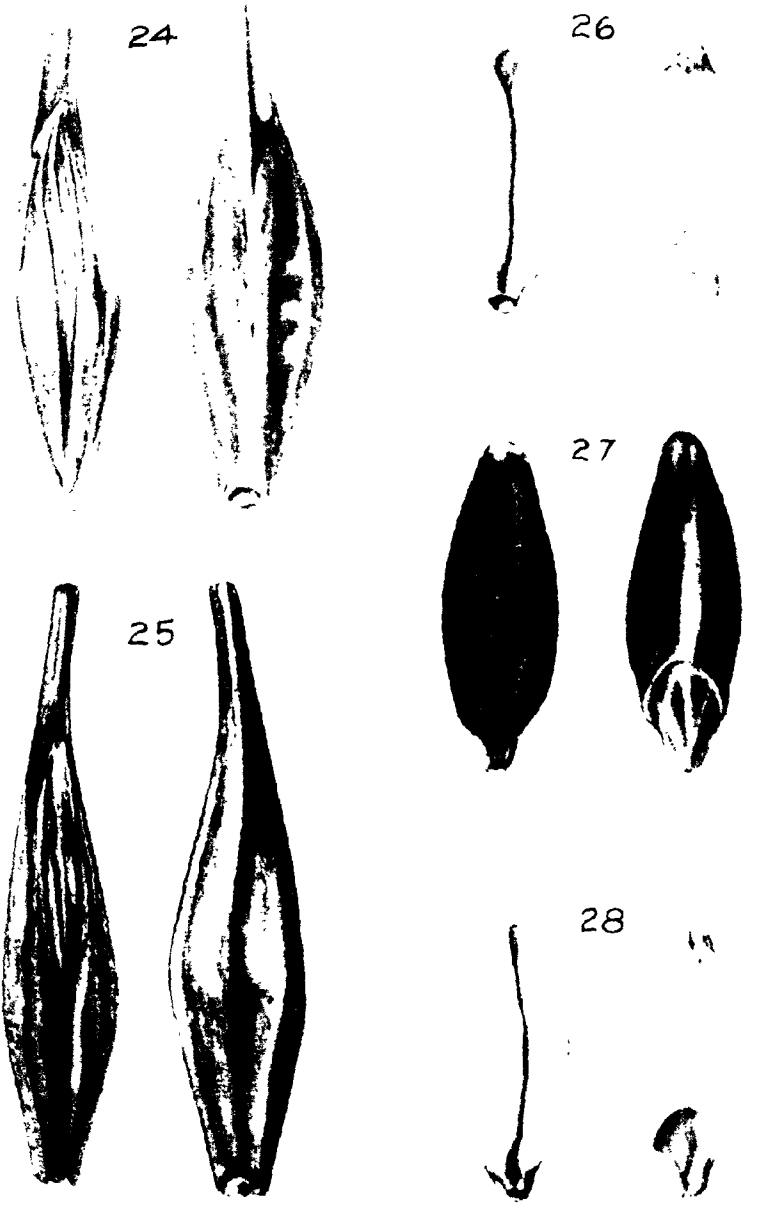
VARIETIES OF HORDEUM VULGARE, H. INTERMEDIUM, AND H. DISTICHON

H. vulgare, 12, Black Hulless, 13, White Hulless
H. intermedium, 14, Arlington Awnless, 15, S. P. I. 40326
H. distichon, 16, Hanna, 17, Chevalier



VARIETIES OF HORDEUM DISTICHON

18, Manchuria x Vermont Champion. 19, Goldthorpe. 20, Amatou on Black. 21, Black Two-rowed. 22, Naked Spring. Selected [illegible]



VARIETIES OF HORDEUM DEFICIENS

24, Russian Courland; 25, Selection 621; 26, S. P. I. 41155; 27, Selection 626; 28, Nepal Hulless

odes of rhachis, nodding; grain black, more or less glaucous, small, awned; awns barbed, medium to long, stiff; lateral nerves barbed; glumes narrow, awn-pointed; rhachilla beset with long, straight hairs. itional specimens of this variety, all of which were very similar in ter. were found under the following names: Asstivum Schwarze rgerste, Leiorrhynchum (Keke.), Nigrum Schwarze Sommergerste. ss (Plate XXXV, 8).— Foliage medium green; culms medium to rect in early growth; early in maturity; spikes lax; length of ten des of rhachis 3.6–3.8 cm., nodding to an angle of 45° to 100°; cm. or more in length, yellow, hulled and hooded, hood usually distance from end of grain; lemma with five rather conspicuous lateral nerves barbed; base of lemma with horseshoe-like depres- ter glumes narrow, awn-pointed, total length about same as hachilla long, narrow, sparsely covered with short hairs.

llowing key separates the subvarieties of the variety Success:

very early in maturing; culms short; heads nodding only slightly; foliage dark n . . . . . Success.
early to medium in maturing; culms medium in length; heads nodding; foliage h . . . . . Virginia Hooded.
[illegible] specimens found under the following names: Beardless, Success Beard- ss, Virginia Selection 64.)

[illegible] Distinguished from Success by having very short, dense .7 1.9 cm. to ten internodes of the rhachis), long, straight hairs, hich never emerges completely from the sheath of the last leaf, maturity. Original specimen unnamed.

Plate XXXV, 9).—Leaves dark green, abundant, rather broad; dium in height and diameter, straight, strong; erect in early las: internode of culm long; medium early in maturity; spike h of ten internodes of rhachis 3.3–3.5 cm., nodding to an angle : grain broad, 0.75–0.9 cm. long, very starchy, white; lemma caryopsis, bearded; beards long, broad, lax, barbed; lemma with like depression; outer glumes narrow, short-awned, total length of grain; rhachilla beset with long, straight hairs.

al specimens of this variety were found under the following pcrulescens Ser., Naked Barley, Naked Spring.

Hulless (Plate XXXV, 10).— Foliage medium green, abundant rowth; culms medium in size and length, with a tendency lging; spike scarcely out of sheath of last leaf at maturity;

semi-winter in early habit of growth; somewhat earlier in maturing than Coeleste; spikes lax, 2.8–3.0 cm. to ten internodes of rhachis, nodding; grain white, short (0.65–0.75 cm.), broad in proportion to length; lemma free from caryopsis, awned; awns medium in length, rather stiff, barbed; lemma with five rather inconspicuous nerves; lateral nerves barbed; outer glumes narrow, short, awn-pointed, total length of glume and awn point slightly greater than length of glumes; rhachilla beset with long, straight hairs.

Additional specimens of this variety were found under the following names: C. I. 703, Sangatsuka.

Guy Mayle (Plate XXXV, 11).— Foliage light green; culms medium to short, weak, showing tendency toward lodging; erect in early growth, spikes entirely emerged from sheath of last leaf; very early in maturing, the earliest of all the hull-less types; spike lax, 3.2–3.5 cm. to ten internodes of rhachis, nodding to an angle greater than 90°; grain blue, pigment present in aleurone layer, 0.75–0.85 cm. long; lemma free from caryopsis, awned; awns barbed, rather broad, stiff; lemma with horseshoe-like depression; outer glumes narrow, short-awned, total length about twice that of lemma; rhachilla beset with long, straight hairs.

Additional specimens of this variety were found under the name Blue Hulless.

Black Hulless (Plate XXXVI, 12).— Foliage medium green; culms medium in length and diameter, with a tendency toward lodging; spikes well out of sheath of last leaf at maturity; erect in early habit of growth; early in maturing; spikes lax, 3.4–3.7 cm. to ten internodes of rhachis, nodding to an angle of 60° to 90°; grain purple, color usually developed to the greatest extent on dorsal side near tip; grain short (0.7 cm. or less), broad in proportion to its length; lemma free from caryopsis, awned; awns straight, parallel, barbed, rather coarse; five nerves of lemma inconspicuous; lateral nerves barbed; lemma usually showing some color development along dorsal nerve; base of lemma with horseshoe-like depression; outer glumes narrow, short-awned, total length about twice that of lemma; rhachilla beset with long, straight hairs.

Additional specimens of this variety were found under the following names: Blaue Excelsior, Blaue Nackte Gerste, Virginia Black Hulless, Violaceum.

Italian Hulless.— Foliage medium green; culms medium to short, large in diameter; erect in early growth; spikes well out of sheath of last leaf

t maturity; medium to early in maturity; spikes very lax, 4.2–4.4 cm. o ten internodes of rhachis; angle of inclination of kernel with rhachis, ery small; grain white, long (0.8–1.0 cm.), narrow; lemma free from aryopsis, awned; awns 10 cm. or more long, barbed, rather stiff; five ierves of lemma rather conspicuous, lateral nerves barbed; base of lemma vith horseshoe-like depression; outer glumes short, narrow, awns pointed, otal length about same as that of lemma; rhachilla sparingly beset with hort, recurved hairs.

S. P. I. 41156.— Foliage dark green; culms medium to short; semi-vinter in early growth; late in maturity; spikes lax (3.0–3.4 cm. to ten nternodes of rhachis), but usually erect; grain yellow, short (0.6–0.7 m.), broad in proportion to its length; lemma free from caryopsis, awned; wns less than 5 cm. long, narrow, barbed, stiff; five nerves of lemma ather conspicuous, lateral nerves barbed; outer glumes narrow, short, wn-pointed, total length about the same as that of lemma; rhachilla eset with short, recurved hairs.

S. P. I. 41157.— Foliage medium green; culms medium to short; rect in early habit of growth; spikes well out of sheath of last leaf at naturity; medium to early in maturity; spikes erect or only slightly odding, dense (2.2–2.4 cm. to ten internodes of spikelet); grain blue, igment present in aleurone layer; grain 0.7 cm. or less in length, more han half as broad as long; lemma free from caryopsis, awned; awns arbed; base of lemma cross-creased; outer glumes narrow, awn-pointed, otal length about one and one-half times that of lemma; rhachilla beset vith long, straight hairs.

White Hulless (Plate XXXVI, 13).— Foliage dark green, broad; culms arge, coarse, medium to tall; somewhat spreading in early growth, but nclined to lodge easily; spikes scarcely emerging from sheath of last leaf, ccasionally emerging from side of sheath; medium in maturity; length f 10 internodes of spike over 3.0 cm.; spikes nodding from 10° to 90°; rain white to yellow, 0.7–0.8 cm. in length, about half as broad as long; emma free from caryopsis, hooded, hoods set close to end of kernel; five ierves of lemma rather conspicuous, lateral nerves barbed; base of lemma ossessing horseshoe-like depression; outer glumes narrow, awn-pointed, otal length about the same as that of lemma; rhachilla beset with long, traight hairs.

Additional specimens of this variety were found under the following ame: C. I. 595, Hulless, Nepal.

Selection 308.— Foliage medium green; culms rather short, coarse; erect in early habit of growth; spikes emerging from side of leaf sheath, late in maturity; spikes very dense and erect; grain black, long, narrow; lemma black, free from caryopsis, hooded; five nerves of lemma conspicuous, lateral nerves barbed; base of lemma cross-creased; rhachilla beset with long, straight hairs. Original specimen unnamed.

HORDEUM INTERMEDIUM

Hordeum intermedium (fig. 68) is similar to *H. vulgare* in most characters. It may be briefly described as follows:

Nodes of rhachis solidified; spikes nodding and lax in most cases; spikelets arranged in groups of three at each node of rhachis, all sessile, all fertile, median spikelet awned (fig. 51, C, and D, and fig. 68) or hooded (fig. 69), lateral spikelets neither awned nor hooded; grain of lateral spikelets one-half to two-thirds as large as grain of median spikelets; grain varying in color and in adherence of lemma to caryopsis.

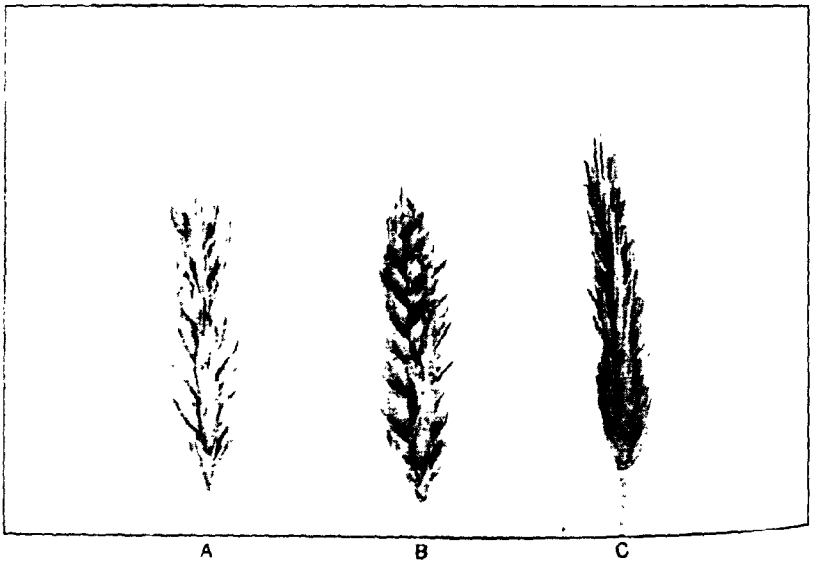


FIG. 68. TYPES OF HORDEUM INTERMEDIUM

A, Arlington Awnless; B, South African Nepal Hulless; C, S. P. I. 40326

FIG. 69. COMPARISON OF SPIKELETS AT ONE NODE OF RHACHIS OF HULL-LESS TYPE OF HORDEUM VULGARE AND OF H. INTERMEDIUM

Above, dorsal and ventral views of *H. vulgare*; below, dorsal and ventral views of *H. intermedium*

This species is of limited importance, from an economic standpoint, both in the United States and in Europe. One variety, Arlington Awnless, is of some importance along the southern border of the barley-producing section of the United States.

The varieties belonging to this species are probably of hybrid origin for the most part, and have been in existence for only a short time. As an illustration, Derr (1911) gives an account of the hybrid origin of Arlington Awnless.

Key to varieties of H. intermedium

A. Kernels hulled. PAGE
  B. Lemmas of central spikelets awned.
    C. Kernels white, blue, or purple.
      D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.5 cm. to ten internodes); base of lemma with horseshoe-like depression.
        E. Rhachilla beset with long, straight hairs.
          F. Awns short, barbed.
            G. Semi-winter habit of early growth.
              HH. Pigment present in aleurone layer, light blue
                Arlington Awnless 432
    CC. Kernels black.
      D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.5 cm to ten internodes); base of lemma with horseshoe-like depression.
        E. Rhachilla beset with long, straight hairs.
          F. Awn short, barbed.
            G. Semi-winter habit of early growth . . . . . S. P. I. 40326. 433
AA. Kernels hull-less.
  BB. Lemmas of central spikelets hooded.
    C. Kernels white, blue, or purple.
      D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.5 cm to ten internodes); base of lemma with horseshoe-like depression.
        E. Rhachilla beset with long, straight hairs.
          F. Spring habit of early growth.
            G. No pigment in aleurone layer, white or yellow. . .
              Nepal Hulless 433

Descriptions of varieties

Arlington Awnless (Plate XXXVI, 14).— Foliage medium green, culms medium to short, small in diameter; semi-winter in early habit of growth; spikes only slightly emerged from sheath of last leaf; medium in maturity; spikes lax (3.0–3.4 cm. to ten internodes), nodding only slightly; grain light blue, pigment present in aleurone layer; grain of median spikelet medium to small in size, grain of side spikelets only slightly more than half the size of that of median spikelet; lemma adhering closely to caryopsis, lemma of median spikelet short-awned (never more than 1.5 cm.), lemmas of side spikelets blunt; five nerves of lemma inconspicuous

lateral nerves barbed; base of lemma horseshoe-shaped; outer glumes narrow, awn-pointed; rhachilla beset with long, straight hairs.

Specimens of this variety found under the following names: C. I. 702, Cornell Selection 1, Cornell Selection 8, Cornell Selection 9.

S.P.I. 40326 (Plate XXXVI, 15).—The variety S. P. I. 40326, which is probably a selection from the original cross that produced Arlington Awnless, differs from the latter by possessing black-colored grains.

Nepal Hulless (Plate XXXVIII, 28).—Foliage medium green; culms short but rather large in diameter; erect in early growth, stooling very little; medium in maturity, maturing just ahead of Arlington Awnless; spikes lax, 3.0–4.0 cm. to ten internodes of rhachis, nodding, short; grain white; grain of median spikelet medium to small, grain of side spikelets about two-thirds as large as grain of median spikelet; lemma free from caryopsis, lemma of median spikelet hooded, lemmas of side spikelets blunt to awn-pointed, point never more than 1 cm. long; five nerves of lemma inconspicuous, lateral nerves barbed; outer glumes narrow, awn-pointed; rhachilla beset with long, straight hairs.

HORDEUM DISTICHON

Hordeum distichon is distinguished from *H. vulgare* and *H. intermedium* in the character of fertility. *H. distichon*, like *H. spontaneum*, has only the central spikelet of the three spikelets at each node of the rhachis fertile, while *H. vulgare* and *H. intermedium* have all three spikelets fertile. The lateral spikelets of *H. distichon*, although infertile, have all the floral organs, including outer glumes, lemma, palea, and rudimentary sexual organs. The same variations in density of spikes (fig. 70), terminal appendages (fig. 71), rhachillas, size, shape, and color of kernels, barbing of lateral nerves, color of lemmas, and adherence of flowering glume (fig. 71), are found in this species as are found in *H. vulgare*, and for this reason a detailed description of these variations need not be given here.

H. distichon is of equal importance economically with *H. vulgare*, although it is not grown as extensively in the United States. It is the leading barley for malting purposes in European countries. The extensive production of varieties of this species in the United States is limited to North Dakota and South Dakota, but it is grown to some extent over the entire barley-producing region.

FIG. 70. THREE STAGES OF DENSITY IN HORDEUM DISTICHON

A, Fan Barley. B, Goldthorpe. C, Chevalier

Key to varieties of H. distichon

A. Kernels hulled.
B. Lemmas awned. PAGE
C. Kernels white, blue, or purple
D. Spike narrow, lax, nodding, internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression
E. Rhachilla beset with long, straight hairs.
F. Awns barbed from base to tip
G. Spring habit of early growth.
H. Lateral nerves smooth Hanna 436
HH. Lateral nerves barbed
I. No pigment in aleurone layer, white or yellow Vermont Champion 438
II. Pigment present in aleurone layer, dark blue Turkish Smyrna 438
FF. Awns smooth at base for greater or less distance.
G. Spring habit of early growth.
H. Lateral nerves smooth ..... Smyrna. 438
EE. Rhachilla beset with short, more or less recurved hairs.
F. Awns barbed from base to tip.
G. Spring habit of early growth.

PAGE

H. Lateral nerves smooth.
I. Spike unbranched ..... Chevalier. 439
II. Spike branched ..... Wessling. 439
HH. Lateral nerves barbed.
I. No pigment in aleurone layer, white or yellow
Manchury x Vermont Champion. 440
II. Pigment present in aleurone layer, dark blue
Turkish Syrian. 440
FF. Awns smooth at base for greater or less distance.
G. Spring habit of early growth.
HH. Lateral nerves barbed.
I. No pigment in aleurone layer, white or yellow
Syrian. 440
DD. Spike broad, compact, usually nearly erect, internodes of rhachis short (2.3–3.0 cm. to ten internodes); base of lemma cross-creased.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
H. Lateral nerves smooth; density greater than 2.2 cm. to ten internodes of rhachis; spike of uniform width from base to tip Goldthorpe. 440
HH. Lateral nerves barbed, density less than 2.2 cm. to ten internodes of rhachis; spikes broader at base than at tip, fan-shaped Fan Barley. 441
EE. Rhachilla beset with short, more or less recurved hairs.
F. Awns barbed
G. Spring habit of early growth.
H. Lateral nerves smooth, density greater than 2 cm. to ten internodes of rhachis Primus. 441
CC. Kernels black or containing black pigment.
D. Spike narrow, lax, nodding, internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
HH. Lateral nerves barbed Anatolian Black. 442
EE. Rhachilla beset with short, more or less recurved hairs.
F. Awns barbed.
G. Spring habit of early growth.
H. Lateral nerves smooth ..... Black Two-rowed. 442
BB. Lemmas hooded
CC. Kernels black or containing black pigment.
D. Spike narrow, lax, nodding, internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
EE. Rhachilla beset with short, more or less recurved hairs.
F. Spring habit of early growth
G. Lateral nerves barbed ..... Ingrescens. 442
AA. Kernels hull-less.
B. Lemmas awned.
C. Kernels white, blue, or purple.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.

PAGE

G. Spring habit of early growth.
HH. Lateral nerves barbed.
I. No pigment in aleurone layer, white.....Naked Spring. 443
II. Pigment present in pericarp layer, purple.....
S. P. I. 41153. 443

DD. Spikes very broad, compact, erect; internodes of rhachis very short (1.6–2.1 cm. to ten internodes); base of lemma cross-creased.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
HH. Lateral nerves barbed.
I. No pigment in aleurone layer, white or yellow
Selection 614. 443

BB. Lemmas hooded.
C. Kernels white, blue, or purple.
DD. Spike very broad, compact, erect; internodes very short (1.6–2.1 cm. to ten internodes); base of kernel cross-creased.
E. Rhachilla beset with long, straight hairs.
F. Spring habit of early growth.
GG. Lateral nerves barbed.
H. No pigment in aleurone layer, white or yellow
Selection 616. 443

CC. Kernels black.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
EE. Rhachilla beset with short hairs.
F. Spring habit of early growth.
G. Lateral nerves smooth. Selection 607. 441

Descriptions of varieties

Hanna (Plate XXXVI, 16).—Foliage medium green; culms rather long, slender, often lodging under adverse weather conditions; erect in early habit of growth; spike usually well out of sheath of last leaf; medium to late in maturity, later than most of the common six-rowed barleys; spikes lax, nodding, length of internodes varying from 3.3 to 4.1 cm. with an average length of from 3.6 to 3.8 cm.; grain rather short (9 mm.), very plump, symmetrical; lemma and palea cross-wrinkled, yellow in color, often darker at base; awns long, more or less spreading; five nerves of lemma more or less conspicuous, lateral nerves smooth; base of lemma with a slight horseshoe-like depression; rhachilla beset with long, straight hairs.

The following subvarieties may be distinguished within the Hanna variety. These divisions cannot be made with absolute certainty, however, as the differences are in degree and are naturally more or less indefinite. Such characters as height and maturity, as already explained, cannot be relied upon because of variations produced under different conditions.

FIG. 71. VARIATION IN TERMINAL APPENDAGE AND ADHERENCE OF LEMMA. A, Hanna; B, *Hordeum intermedium*; C, Naked Spring; D, *H. vulgare nudum*.

A. Foliage light green, very early maturity, short culms . . . . . Selection 123.
AA. Foliage medium to dark green; culms medium to long. . . . . Hanna.
B. Medium to early in maturity . . . . .

(Considerable variation occurs here both in maturity and in attitude of the spike. In general, the specimens named *Hannchen* are somewhat earlier in maturity, and possess a slightly denser spike which droops to a greater angle, than the true Hanna).

(Additional specimens of the subvarieties Selection 423 and Hanna found under the following names: Abed Binder, Ackermans Niedebayrische, Austin Hanna, Australian, Australian Early, Australian Hollischauer, Australian Loosdorfer, Austrian Hanna, Austrian Proskowetz, Bavarian, Bayerische Landgerste, Bohemia, California Chevalier, California Moravian, Canadian, Chevalier, Chinese (King Kua), Frankergerste Stamm, French, German, German Bavaria, German Hanna, German Heils Granken, German Nole Early, Gold Foil, Hanakische Gerste, Hansche, Hungarian Hanna, Hungarian Loosdorfer, Japanese, Kwassitzer Hanna, Lechrainer, Loosdorfer, Mahrische, Niederbayerische Landgerste, Noles Bohemia, Proskowetz, Pure Bred Spring, Roumanian Chevalier, Roumanian Common, Roumanian Hanna, Rud. Bethges, Scottish Lothian Chevalier, Seehsanter, Steigum, Svalof, Svalof Hannchen, Swedish Gold, Swedish Gotland, Swedish Oland, Swiss Spring, Two-rowed Black, Zeiness Vered.)

BB. Late to very late in maturity, a much greater constant difference between this subvariety and Hanna than between Hanna and Hannchen Princess.

(Additional specimens of this subvariety found under the following names: Heines Verbessert Chevalier, Italian, Mahndorfer, Netherlands, Svalof Princess, Swedish Princess, Unterfrankische Zuchtaus-schussgerste.)

Vermont Champion.— The variety Vermont Champion has the same general characteristics as has the variety Hanna, except that barbs appear on the lateral nerves of the lemma. Some variation in the degree of barbing has been found, but during the period of the present study the specimens named below have always been found to have some barbs present.

Additional specimens of this variety were found under the following names: Chiligerste, French, German Bavaria, Gerste aus dem Banat, Hanna x Vermont Champion, Jerusalem Gerste, Jutlandische Gerste, Swedish Oland, Ungarische Hanna.

The specimen named Hanna x Vermont Champion was somewhat taller and a little denser than the other subvarieties.

Turkish Smyrna.— Foliage medium green; number of nodes in culm small; culms short; erect in early growth; spikes scarcely emerged from sheath of last leaf; early in maturity; spikes medium in length, lax, nodding; internodes of rhachis long (3.5 4.2 cm. to ten internodes); grain large, dark blue; lemma closely adhering to caryopsis, usually discolored, awned; awns barbed from base to tip; nerves of lemma barbed; base of lemma with horseshoe-like depression; outer glumes awn-pointed, extending just beyond lemma; rhachilla beset with long, straight hairs, the hairs occasionally rather sparse.

Additional specimens of this variety were found under the following names: Syrian, Turkish (Smyrna Highland).

Smyrna. The variety Smyrna is distinguished from Turkish Smyrna by possessing (1) awns which are only partly barbed, the barbs appearing

at the tip of the awn and extending from one-third to two-thirds of the distance to the base of the awn, the base of the awn being perfectly smooth, (2) smooth lateral nerves, and (3) nonpigmented grain.

The following key separates the subvarieties of the variety Smyrna:

A. Culms short; early in maturity . . . . . Smyrna.
(Additional specimens found under the following names: African (Anatolia), Australian Hollischauer (Hanna), California Chevalier, Ouchac, Smyrna 521, Turkish, Turkish Afrokarchissar, Turkish Anatolian, Turkish Smyrna Highland.)

AA. Culms medium to long; medium to late in maturity . . . Schaley's.

Chevalier (Plate XXXVI, 17). — The variety Chevalier is distinguished from Hanna only by the characters of the rhachilla. The rhachilla not only is beset with short, fine hairs which are more or less recurved at the tip, but is about one-half longer in Chevalier than in Hanna. Otherwise the two varieties seem exactly the same in adaptation as well as in observable morphological characters.

The names as applied to these two varieties might be reversed and still be just as correct. The only reason for applying them as they are applied is because more specimens with the name *Hanna* attached appeared with the characteristics of Hanna as here given, than appeared with the characteristics of Chevalier as here given; while no specimens appeared with the name *Hanna* with the Chevalier characters.

The following key separates the subvarieties of the variety Chevalier:

A. Foliage dark green, broad, very early in maturity . . . Bavarian.
(An additional specimen found under the name Rieser Gerste.)

AA. Foliage medium green, average width; medium to late in maturity . . . Chevalier.
(Additional specimens found under the following names: Australian, Balton, Bergstrassen, Bohemian, California Chevalier, Challenge, Chevalier (Knavers, Chilian Chevalier, English Chevalier, Golden Drop, Gold Foil, Gold Melonen Chevaliergerste, Horn, Idaho, Manchuria, New Zealand, Pfelzer, Probsteier Perlgerste, Scottische Annat, Scottische Perlchevaliergerste, Scottish Chevalier, Silver King, South African Golden Grain, Tasmanian Battledore. The specimen named *Balton* was found to be more dense (3.0–3.2 cm. to ten internodes) than the others of this group.)

Wessling. — The variety Wessling differs from other two-rowed barleys by possessing (1) a more or less branched spike and (2) a triplication of spikelets at some of the nodes. In this variety, instead of one set of three spikelets, one fertile and two sterile, there are at a number of nodes near the base of the spike three sets, thus giving three fertile and six sterile spikelets at one node. In some cases, also, a secondary rhachis is produced in the place of the fertile median spikelets. This secondary rhachis then

bears three spikelets at each node, all of which arise on the outer side. In other morphological characters this variety is similar to Chevalier.

The original specimen name was Wessling's Trounengerste.

Manchury x Vermont Champion (Plate XXXVII, 18).— The variety Manchury x Vermont Champion is distinguished from Chevalier by the presence of barbs on the lateral nerves. This difference has been found to be constant, although the degree of barbing varies to some extent with different seasons. This group has the same adaptations as Chevalier but has not been grown so extensively.

The following key separates the subvarieties of the variety Manchury x Vermont Champion:

A. Kernels medium-sized; awns rather fine, more or less deciduous ... Manchury x Vermont Champion.
(Additional specimens of this variety found under the following names: Austrian, California Chevalier, Chevalier, German, Noles Moravia Chevaliergerste, Princess, Svalöf Chevaliergerste, Swedish Chevalier II.)

AA. Kernels very large, awns coarse, showing no tendency toward deciduousness ... Selection 503.

Turkish Syrian.— Foliage medium green; culms very short; erect in early growth; spikes failing to emerge completely from sheath of last leaf; early in maturity but somewhat uneven; spikes short, erect; internodes of rhachis long (3.5–3.8 cm. to ten internodes); grain rather long but not plump; aleurone layer pigmented, dark blue; lemma adhering tightly to caryopsis, awned; awns barbed for entire length; lateral nerves of lemma barbed; base of lemma with horseshoe-like depression; outer glumes narrow, awn-pointed, scarcely extending beyond lemma; rhachilla beset with short hairs.

Syrian.— Distinguished from Turkish Syrian by possessing (1) awns barbed from one-third to two-thirds the distance from tip to base, the base being perfectly smooth, and (2) nonpigmented grain.

Goldthorpe (Plate XXXVII, 19).— Foliage medium green; culms long; leaves rather broad, abundant; erect in early growth; very late in maturity; side spikelets somewhat more developed than in Chevalier; spike dense, length of ten internodes 2.0–3.0 cm.; angle of inclination of kernels with rhachis, great, making spike broad; spikes same width from base to tip, nodding to considerable extent but not so much as in laxer types already described; grain white, long, rather broad; lateral nerves forming rather prominent shoulders; palea and lemma not so much cross-wrinkled as in

more lax types; lemma adhering closely to caryopsis, rather coarse, awned; awns barbed, long, spreading; nerves of lemma conspicuous, smooth; base of lemma cross-creased; outer glumes awn-pointed; rhachilla beset with long, straight hairs; rhachis in some cases more or less articulate at nodes.

Two important commercial subvarieties of Goldthorpe, Svanhals and Goldthorpe, have only one distinguishing characteristic, which is one of degree and not absolutely reliable: Svanhals is a few days later in maturity than Goldthorpe.

Additional specimens of Goldthorpe were found under the following names: Australian, Bavarian, Bestehorns Diamant, Bestehorns Kaiser, Böhmische Gerste, Chile, Frederiksons Gerste, Hungarian, Imperial, Jewel, Moravian, New Burton Malting, Norwegian Imperialleyg, Scottish Lothian Standwell, Spiegelgerste aus Utuna, Virginia Selection 4, Virginia Selection 7, Webbs Bartlose.

Additional specimens of Svanhals were found under the following names: Goldthorpe, *Hordeum distichum nutans*, Noles Imperialgerste Type A, Svalof's Svanhals, Svalof's Swanneck, Virginia Selection 647.

Fan Barley.—Foliage medium green; culms medium to short, rather large in diameter; erect in early growth; spikes scarcely emerging from sheath of last leaf; earlier than other erect types of two-rowed barleys; side spikelets infertile but large, containing rudimentary pistils; spike short, very dense (length of ten internodes of rhachis less than 2.2 cm.), broader at base than at tip; angle of inclination of kernels with rhachis, very great at base, decreasing toward tip; spike very erect; grain white or yellow, medium to large, lemma adhering closely to caryopsis, awned; awns barbed, very spreading, giving the general appearance of a fan; lateral nerves of lemma barbed; base of lemma cross-creased; outer glumes short-awned, extending at least to twice length of lemma; rhachilla beset with long, straight hairs.

Additional specimens of this variety were found under the following names: *Hordeum distichum*, Pfauengerste.

Primus.—Distinguished from Goldthorpe in that the rhachilla is beset with short, more or less recurved hairs, rather than with long, straight hairs.

Additional specimens of this variety were found under the following names: Australian, Breustedts Horzer Gerste, Fruhwirts Fruhe Goldthorpe, *Hordeum distichum erectum*, New Burton Malting, Standwell,

Svalöf's Primus, Swedish Upland, Tasmanian, Tasmanian Ideal, Upland. The specimens under the second and third names are somewhat earlier than the others.

Anatolian Black (Plate XXXVII, 20).— Foliage medium green; culms short to medium in length; leaves rather short, narrow; erect in early growth; stooling very little; spikes scarcely emerging from sheath of last leaf; medium to early in maturity; spikes lax, nodding to only a small angle; kernels forming only a slight angle of inclination with rhachis; grain rather large, long, brown to black, black pigment in both pericarp and glumes; lemma adhering closely to caryopsis, awned; awns and lateral nerves barbed; base of lemma with horseshoe-like depression; outer glumes awn-pointed; rhachilla beset with long, straight hairs.

An additional specimen of this variety was found under the name Asia Minor.

Black Two-rowed (Plate XXXVII, 21).— Foliage light green; leaves large, broad, long; culms long, medium in size; erect in early growth; stooling well; spikes completely emerging from sheath of last leaf; late in maturity; spikes lax, long, nodding; grain black, pigment in both glumes and pericarp; lemma adhering closely to caryopsis, awned; awns long, more or less pigmented, barbed, somewhat spreading; lateral nerves smooth, conspicuous, forming prominent shoulders; base of lemma with horseshoe-like depression; outer glumes narrow, awn-pointed; rhachis beset with short hairs.

Additional specimens of this variety were found under the following names: *Hordeum distichum erectum*, Schwarze Zweizeilige Gerste.

Ingrescens.— Foliage medium to dark green, abundant; culms tall; spikes lax, nodding; grain black or dark brown, large; lemma closely adhering to caryopsis, hooded; hoods small, set on short awns; lateral nerves barbed; base of lemma with horseshoe-like depression; outer glumes awn-pointed, narrow; rhachilla often reduced, beset with short hairs.

This variety is of no economic importance. Only two specimens were obtained, which may be separated by the following key:

A. Very late in maturing; foliage dark green; leaves very broad; spikes very long, grain large . . . . . Type I.

AA. Medium in maturity; foliage medium green; leaves only slightly broader than the average for barley; spikes medium in length, grain medium in size . . . . . Type II.

Naked Spring (Plate XXXVII, 22).— Foliage dark green; culms short and weak, with strong tendency toward lodging; erect in early growth; early in maturity; spikes lax, long, nodding; grain white, very large, almost oval in shape; lemma free from caryopsis, awned; awns very long, barbed; lateral nerves of lemma barbed; base of lemma with horseshoe-like depression; rhachilla beset with long, straight hairs.

An additional specimen of this variety was found under the name Gerste aus der Krim.

S. P. I. 41153.— Foliage medium green; culms medium to short; erect in early growth; average in maturity; spike of medium length, usually erect; grain small, purple; lemma free from caryopsis, slightly pigmented, short-awned; awns and lateral nerves of lemma barbed; rhachilla beset with long, straight hairs.

An additional specimen of this variety was found under the name S. P. I. 41162.

Selection 614.— Foliage dark green; culms short, rather large; erect in early growth; medium in maturity; spikes dense, broad, short, erect, emerging from side of leaf sheath; grain nonpigmented, oval, medium in size; lemma free from caryopsis, awned; awns very spreading, barbed; nerves of lemma barbed; rhachilla beset with long, straight hairs.

This variety is of no economic importance at present.

Selection 616.— Foliage very dark green; culms short, large; leaves very short, broad; medium in fertility; spikes very short, broad, emerging far down side of leaf sheath; side spikelets very large but infertile; grain nonpigmented, large; lemma free from caryopsis, hooded; nerves of lemma barbed; rhachilla beset with long, straight hairs.

This variety is of no economic importance at present.

Selection 607 (Plate XXXVII, 23).— Foliage dark green; culms medium to tall; erect in early growth; late in maturity; spikes long, narrow, nodding; internodes short; grain black, narrow but medium in length; lemma free from caryopsis, hooded; lateral nerves barbed, rhachilla beset with short hairs. This variety is of no economic importance at present.

HORDEUM DEFICIENS

Hordeum deficiens (probably first described as *H. decipiens*) is distinguished from *H. vulgare* and *H. intermedium* by the sterile side spikelets,

and from *H. distichon* by a great reduction in the structures of the side spikelets. The side spikelets of *H. deficiens* (fig. 72) not only are sterile, but also are reduced in all the floral parts to a much greater extent than in *H. distichon*. In some cases all that remains in evidence of a side spikelet is one outer glume. Neither pistil nor stamens are ever present

FIG. 72.—VARIOUS TYPES OF HORDEUM DEFICIENS

A, Selection 621, B, Russian Courland; C, S. P. I. 41155, D, Selection 626, E, Selection 625

H. deficiens has not become of economic importance in the United States. Abyssinia is the source of practically all the varieties belonging to this species.

Key to varieties of H. deficiens

A. Kernels hulled
  B. Lemmas awned
    C. Kernels white, blue, or purple.
      D. Spike narrow, lax, nodding, internodes of rhachis long (3.0–4.1 cm. ten internodes), base of lemma with horseshoe-like depression.

E. Rhachilla beset with long, straight hairs. PAGE
F. Awns barbed.
G. Spring habit of early growth.
H. Lateral nerves smooth. . . . . Russian Courland. 445
EE. Rhachilla beset with short hairs.
F. Awns barbed.
G. Spring habit of early growth.
HH. Lateral nerves barbed, outer glumes very broad
Selection 44. 446
CC. Kernels black.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
HH. Lateral nerves barbed . . . . . Selection 621. 446
EE. Rhachilla beset with short hairs.
F. Awns barbed.
G. Spring habit of early growth.
HH. Lateral nerves barbed . . . . . Selection 622. 446
BB. Lemmas hooded.
CC. Kernels black.
D. Spike narrow, lax, nodding; internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Spring habit of early growth.
G. Lateral nerves smooth. . . . . Selection 657. 446
AA. Kernels hull-less.
B. Lemmas awned.
C. Kernels white, blue, or purple.
D. Spikes narrow, lax but erect, internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Awns barbed.
G. Spring habit of early growth.
HH. Lateral nerves barbed . . . . . S. P. I. 41155. 446
BB. Lemmas hooded.
C. Kernels white, blue, or purple.
D. Spike broad, erect, but internodes of rhachis long (3.3–3.6 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Spring habit of early growth.
GG. Lateral nerves barbed, lemma seven-nerved. . . . Selection 625. 447
CC. Kernels black.
D. Spike narrow, lax, slightly nodding; internodes of rhachis long (3.0–4.1 cm. to ten internodes); base of lemma with horseshoe-like depression.
E. Rhachilla beset with long, straight hairs.
F. Spring habit of early growth.
GG. Lateral nerves barbed. . . . . Selection 626. 447

Descriptions of varieties

Russian Courland (Plate XXXVIII, 24, and fig. 72, B).—The variety Russian Courland is characterized by the same general appearance and

adaptation as Hanna, in *H. distichon* species, with the one exception of the development of the side spikelets. In this variety these are very rudimentary, consisting only of the outer glumes and a very small, undeveloped lemma without palea or pistil.

An additional specimen of this variety was found under the name Early Chevalier.

Selection 44.— Foliage dark green; erect in early growth; spikes emerging from side of sheath of last leaf, rather lax but broad and nearly erect; grain nonpigmented, usually somewhat discolored at base; lemma adhering closely to caryopsis, base with horseshoe-like depression; awns short, broad; outer glumes of median spikelet half as broad as lemma, short-awned; lateral spikelets much reduced, with outer glumes awn-pointed and one-third width of outer glumes of median spikelet; rhachilla beset with short hairs.

Selection 621 (Plate XXXVIII, 25, and fig. 72, A).— Foliage dark green; culms average in height; erect in early habit of growth; spike lax, nodding; grain black, glaucous; lemma adhering closely to caryopsis, awned; awns barbed; lateral nerves barbed; outer glumes very pubescent, awn-pointed; rhachilla beset with long, straight hairs.

Selection 622.— Foliage medium green; culms average in height; erect in early habit of growth; late in maturity; spike lax, nodding; rhachis showing strong tendency toward brittleness; grain black, medium to large; lemma adhering closely to caryopsis, awned; awns black, barbed; lateral nerves barbed; outer glumes small, black, glabrous, awn-pointed; rhachilla beset with short hairs.

Selection 657.— Foliage dark green; leaves broad; culms average in height; semi-winter in habit of early growth; late in maturity; spike lax, nodding; grain black, more or less glaucous; lemma adhering closely to caryopsis, hooded, hoods set on short awns; outer glumes very narrow, short, blunt; lateral nerves of lemma smooth; rhachilla beset with long, straight hairs.

S. P. I. 41155 (Plate XXXVIII, 26, and fig. 72, C).— Foliage medium green; culms short; erect in early growth; early in maturity; spike lax, nodding, short; grain short, broad, nonpigmented; lemma free from caryopsis, awned; awns broad, barbed; lemma occasionally possessing an extra pair of lateral nerves; outer glumes narrow, long, awn-pointed, lateral nerves barbed; rhachilla sparingly beset with straight, rather short hairs.

Selection 625 (fig. 72, E).— Foliage dark green; leaves broad; culms large, coarse, but medium in length; erect in early growth; spikes emerging from side of sheath of last leaf; late in maturity; spikes broad, nearly erect, ten internodes 3.3–3.6 cm. in length; angle of inclination of kernel with rhachis, rather large; grain long, narrow, nonpigmented; lemma adhering closely to caryopsis, hooded; lemma possessing an extra pair of lateral nerves; rhachilla beset with long, straight hairs.

Selection 626 (Plate XXXVIII, 27, and fig. 72, D).—Foliage dark green; culms medium to long; erect in early growth; late in maturity; spikes narrow, lax, nodding; grain black, large; lemma seven-nerved, hooded, hoods sessile; lateral nerves barbed; outer glumes awn-pointed, narrow, very pubescent; rhachilla beset with long, straight hairs.

SUMMARY

In the classification presented in this paper, sixty varieties have been distinguished in the four cultivated species of barley, as follows: twenty-nine in *Hordeum vulgare*; three in *H. intermedium*; twenty in *H. distichon*; and eight in *H. deficiens*. The varieties in each species are systematically arranged accordingly to stable morphological characters — the same characters being used in the separations within each species — and as far as possible according to natural adaptation. An attempt has been made to avoid placing varieties with similar adaptations but with one or more distinct morphological differences too far apart in the key. This, however, could not be avoided in a few instances. The varieties as described are separated by one or more morphological characters which have proved constant for a period of five years under New York environment and which are probably constant under all environmental conditions. For this reason, the keys to the varieties should prove effective in the identification of specimens, at least within narrow limits, in a wide range of conditions. However, the divisions within the varieties as given in the keys to subvarieties are based on more variable characters, and therefore cannot be relied upon in a given environment until proved.

The naming of varieties, as given in the keys, is not an attempt to standardize the nomenclature, as this cannot be done by the efforts of one individual. The choice of a name for a given variety was based on the following rules in the order given: (1) the frequent occurrence of a well-known name; (2) names indicating geographical origin; (3) descriptive

names; and (4) names of producers, discoverers, or introducers. In cases in which no name was given and the specimen was separated on the basis of some stable morphological character, selection numbers were employed.

In conclusion, it should be understood that yield has not been given consideration in the present classification. Without doubt there are represented, among the synonyms of a given variety or subvariety, various strains which differ materially in yield.

ACKNOWLEDGMENTS

The writer wishes to acknowledge the help given him and to express his appreciation of the valuable suggestions and criticisms offered by Professor E. G. Montgomery, of the Department of Farm Crops, Cornell University, under whose direction this investigation was made. He wishes to acknowledge also his indebtedness to Mrs. W. C. Etheridge for the accurate drawings from which the color plates were made, and to C. B. Wiggans for the drawings of the structural parts of the plant.

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OCTOBER, 1921 MEMOIR 47

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

P. W. CLAASSEN

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

P. W. Claassen

In order that the ecological relationships of the insect fauna of the cat-tail plant may be better understood, the first part of this paper deals with the ecology of the cat-tail plant. In the second part, the life history and biology of the insect inhabitants of the plant are discussed. This part of the paper has been treated from a systematic point of view, considering the insects under their respective orders, rather than grouping them according to their life habits. In the résumé, composing the third part, an attempt has been made to bring out the true ecological relationships, grouping the insects with reference to the parts of the plant they affect, their relative importance, and their interrelations

ECOLOGICAL STUDIES OF TYPHA

THE SWAMP AREA OF THE UNITED STATES

According to Davis (1911)[1] there are 139,855 square miles of swamp area in the United States, exclusive of Alaska. This includes bogs, marshes, muck lands, and the more typical swamps. The vegetation in these wet lands varies from the semi-floating forms to the wooded plants of the more solid areas. Needham and Lloyd (1916) state that the bogs, marshes, and swamps "occupy a superficial area larger by far than that covered by lakes and rivers of every sort. They cover in all probably [*sic*] more than a hundred million acres in the United States."

Much of the vegetation of this wet area consists of cat-tail (Typha). Many of the marshes contain an almost pure growth of cat-tail, as, for example, the Montezuma Marsh at the foot of Cayuga Lake. This marsh covers an area of approximately 36 square miles. Although it is impossible to give definite figures on the size of the area occupied by cat-tails in the United States, it is safe to say that there are thousands of square miles of wet lands which are covered by either a pure growth of cat-tail or plant associations in which the cat-tail is the dominant form.

Acknowledgment. The author is indebted to Professor James G. Needham for his helpful suggestions and criticisms in this work.

[1] Bibliographic citations refer to *Literature cited*, page 508.

PLACES OF STUDY

These studies have been made largely from material gathered in the swamps and marshes around Ithaca, New York, especially from Renwick Marsh, at the head of Cayuga Lake. Other collecting places around Ithaca were Michigan Hollow, Mud Creek Swamp, near Freeville, the McLean Bogs, Vanishing Brook, north of the Cornell University campus, Cascadilla Creek, and various other places, wherever cat-tails were found growing. Observations were made also on the extensive cat-tail marshes of Lake Ontario, at North Fairhaven. During the season of 1916–1917, studies on cat-tails were made also in the vicinity of Lawrence, Kansas.

The Renwick Marsh comprises a field of many acres, of which a large proportion is covered with cat-tail. In some places, this plant grows so thickly that all other vegetation is excluded, and especially is this true of the central part of the marsh, where the soil is much wetter. As one approaches the outer margin, other plants mingle with the cat-tails; and at the border, where conditions are drier, the cat-tail growth is sparse. All the cat-tail patches along the Inlet Valley, up to the Buttermilk Falls region, are referred to as the Renwick Marsh.

Michigan Hollow is a swamp located about six miles from Ithaca, in the Inlet Valley. Cat-tails grow here only scatteringly, in small but rather dense patches. This swamp was visited several times to make collections and observations.

In the McLean Bogs, cat-tails are not found in large numbers, but since these bogs were visited every Saturday throughout the spring and summer of 1916, the author was enabled to make more careful and complete observations of the conditions and life histories of the insects of the cat-tail plants there found. Moreover, where cat-tails are not so abundant, a higher percentage of infestation usually occurs, which renders it much easier to obtain material and to make comparative studies.

The Mud Creek Swamp is an old swamp extending along Mud Creek, near Freeville. Here, also, the cat-tails grow but sparingly, but it was found easy and convenient to make frequent observations and collections of material.

Along Vanishing Brook, north of the Cornell University campus, there are a number of small patches of swampy ground, on which cat-tail plants

may always be found. On account of its nearness to the laboratory, this was found to be a convenient place to make some of the observations. Occasional cat-tail plants are also found in Bool's Back Water and in Cascadilla Creek, two places which were likewise chosen for study because their close proximity to the laboratory made daily observations possible.

THE SPECIES OF TYPHA

According to Britton and Brown (1913) there are about ten species of Typha in the temperate and tropical regions of the world. In the United States there are at least two species represented, *Typha latifolia* L (type species) and T. *angustifolia* L. Dudley (1886) lists *T. latifolia* L., var. *elongata*, n. var., as a variety occurring in New York. He describes it as follows: "Leaves very numerous, dark green, elongated (2–3½m.) and fruiting spike elongated, often 30 cm."

Typha latifolia has broad leaves. The staminate and pistillate parts of the flower spike are contiguous. The stigmas are spatulate or rhomboid. Pollen grains occur in fours. Pistillate flowers are without bractlets.

Typha angustifolia has narrower leaves than *Typha latifolia*. The staminate and pistillate flowers of the flower spike are usually separated by a short interval. The stigmas are linear or oblong-linear. Pollen occurs in simple grains. The pistillate flowers have bracts.

Typha is known by the following common names: cat-tail, great reed mace, cat-o'-nine-tail, cat-tail flag, cat-tail rush, flax tail, blackamoor, blackcap, bullsegg, bulrush, watertorch, and candlewick. The names "marsh beetle" and "marsh hog" have also been applied to the Typha plant.

THE DISTRIBUTION OF TYPHA

Cat-tails are common in the temperate and tropical regions of America, South America, Europe, and Asia. Wherever favorable soil conditions occur, cat-tails will be found growing; even a spring on the hillside or the outlet of a drain pipe will sometimes support a few of the plants. Large patches of them grow in the Rocky Mountains, at an altitude of 7500–8500 feet. *Typha latifolia*, the commonest of all the species, occurs throughout the United States in any favorable location. *Typha latifolia* grows abundantly throughout North America, except in the extreme

North. *Typha angustifolia* grows abundantly in the marshes along the Atlantic Coast from Nova Scotia to Florida, as well as inland and even in California.

GROWTH HABIT AND REPRODUCTION

Cat-tails are marsh or aquatic plants, with creeping rootstocks, fibrous roots, and glabrous, erect stems. They are perennial plants, the rootstocks remaining alive while the stem dies down to the ground every year. The following spring these rootstocks, or rhizomes, send up the new plants. Plants which attain only partial growth during the season keep the center alive that winter and probably reach maturity the following summer. The rhizomes spread in every direction and within a few years a large group of cat-tails results from the offsets of a single plant. It is really very difficult to define the limits of a single plant, since they are so linked together by these underground rhizomes (Plate XLV, 56). A two-years growth of a plant, with the connecting rhizome and the offset which will form the next season's stalk, is shown in Plate XL, 18.

Aside from the vegetative mode of increase, Typha produces a great number of seeds each year. These seeds are provided with pappus, which carries them far abroad and insures seeding in all possible situations. In *The Book of Nature Study* (Farmer, 1902: 10), the following statement occurs: "When they [the fruits] become detached from the spike, the hairs borne by the stalk of each fruit act as wings to disperse the seed; the hairs fluff out into downy masses, so that the whole spike looks about a hundred times as large, for a single head will contain a quarter of a million of these flying seeds, according to Professor Lloyd Praeger's estimate."

In order to determine somewhat accurately the number of seeds produced by one head of *Typha latifolia*, the number of seeds in four dry, mature heads was determined. For this work an analytical balance was employed. The procedure was as follows: First, each head was weighed entire, then a small bunch of the seeds was detached and weighed, after which the number of seeds in this bunch was counted; finally, all the seeds were removed and the rachis alone was weighed. From the figures so obtained, the number of seeds in each of the heads was computed (table 1), and the number of seeds in the average Typha head was found to approximate 250,000.

TABLE 1. COMPUTATION OF THE AVERAGE NUMBER OF SEEDS IN EACH TYPHA HEAD

	Sample 1	Sample 2	Sample 3	Sample 4
Length of head (millimeters)	160	180	180	160
Weight of entire head (grams)	35 6735	30 5632	35 2700	27.1150
Weight of rachis (grams)	2 8330	1 9480	2 1610	1.6850
Weight of seeds minus rachis (grams)	32 8405	28.6152	33.1090	25 4300
Weight of detached bunch of seeds (grams)	0 0179	0 0490	0 0400	0 0400
Number of seeds in detached bunch	167	480	300	295
Estimated total number of seeds in head	306,393	280,320	248,317	187,546

Average number for the four heads, 255,644.

GERMINATION OF TYPHA LATIFOLIA

The manner of germination of *Typha latifolia* is very unusual. The development of the plant from the seed was observed in the laboratory. The seeds were placed in watch glasses and could thus be studied under the binocular microscope from day to day. Some of the watch glasses contained only water in which the seeds germinated, while in others a little soil was placed in the bottom in order to observe the growth of the roots. The watch glasses were kept covered to prevent evaporation. The seeds, when first thrown upon the surface of the water, remained floating. Soon, however, the pericarp broke open and the little seeds sank to the bottom.

The seeds are much elongated, pointed at one end and at the other closed by a cone-shaped trapdoor, or cap (Plate XXXIX, 3). The general appearance of the seed is not much unlike some of the insect eggs which are closed at one end with a capsule-like cover. Ten seeds of *T. latifolia*, chosen at random from two heads, were removed from the pericarp and the length and diameter of each was carefully measured (table 2). The average length of the seed was found to be 1.339 millimeters, and the average greatest diameter, 0.307 millimeter. The surface of the seed is sculptured with small, branching ridges, starting at the end of the cap and branching as they run down to the other end. The entire seed, including both its pericarp and its pappus, is about 10 to 12 millimeters long. The pappus consists of from 15 to 20 white hairs, attached to the base and lower quarter of the stalk (Plate XXXIX, 1 and 2).

TABLE 2. MEASUREMENTS OF THE SEEDS OF TYPHA LATIFOLIA

Specimen	Length (millimeters)	Diameter (millimeters)
1	1.50	0.29
2	1.21	0.25
3	1.42	0.28
4	1.35	0.28
5	1.42	0.37
6	1.05	0.28
7	1.42	0.37
8	1.42	0.37
9	1.45	0.28
10	1.15	0.30
Average	1.339	0.307

When germination begins, the cotyledon lengthens and pushes out through the trap door. Sometimes the cap is carried away on the tip of the developing embryo, but more often it remains attached as if by a hinge to the seed. The embryo, immediately after emerging from the seed, turns downward toward the bottom of the dish. Growth is very rapid. Hardly has the embryo come out of the seed before the epidermal cells near the tip begin to send out slender root-hairs, which help to fix the plant to the bottom soil. The other end of the embryo, or cotyledon, remains in the seed, absorbing the reserve starchy material, the only food of the young, developing embryo (Plate XXXIX, 5). When the embryo has become about twice or three times the length of the seed, the growing tip pushes out the first root (Plate XXXIX, 8). The root also bears a number of the root-hairs. With the exception of the ones at the tips of the roots, these root-hairs disintegrate as the plant further develops. At about the same time that the first root appears, the formation of the second leaf may be seen at the crown of the young plant (the outpushing embryo or cotyledon is considered the first leaf). This second leaf soon penetrates the epidermal cells of the first leaf, and comes out to grow and function as a true leaf (Plate XXXIX, 9). After all the food material in the seed has been absorbed, the tip of the first leaf either disintegrates and is thus loosened from the seed, or the tip of the leaf is withdrawn from the seed (Plate XXXIX, 10). The successive stages of the growth of the plant are shown in Plate XXXIX, 4–10.

Not every seed in the head of *Typha latifolia* is perfectly formed or fertile. A number of them never become fully mature, and therefore could not possibly germinate. It is an easy matter to distinguish the fertile seeds in a mature head from the sterile ones. The mature fertile seeds lie in a closely fitting pericarp, while the sterile ones are inclosed in a pericarp which is developed to more than twice the natural size and which has a "hollow" interior with the kernel undeveloped (Plate XXXIX, 1).

In order to determine the approximate percentage of fertility in the seeds of *Typha latifolia*, a number of seeds were picked off at random from several heads and by a careful examination the number of fertile and sterile seeds was determined. The results of these counts are shown in table 3, where it appears that about 75 per cent of the seeds on the mature heads are fertile. The heads from which these counts were made were picked at random and should represent about average conditions. The third head had nearly half of the seeds sterile; the fourth, however, had a high percentage of fertile seeds.

TABLE 3. DETERMINATION OF THE APPROXIMATE PERCENTAGE OF FERTILITY OF TYPHA SEEDS

Head	Number of seeds counted	Number of seeds fertile	Number of seeds sterile	Per cent fertile
1	300	233	67	77 7
2	200	156	44	78 0
3	250	140	110	56 0
4	250	211	39	84 4
Total	1,000	740	260	
Average per cent fertile				74

Having thus ascertained the approximate percentage of fertility in the seeds, experiments were conducted to determine the percentage of germination of the fertile seeds. The seeds were placed in covered watch glasses, and, though kept in the light, were protected from direct sunlight. Germination commenced within a few days after the seeds had been placed in the water. Careful counts were made of the number of seeds

that germinated in each of the watch glasses. The results are shown in table 4. These figures would indicate that not more than two-thirds of the fertile seeds germinate under experimental conditions. Calculating, then, from the percentage of fertility and the percentage of germination, as given in tables 3 and 4, a head containing 250,000 seeds might actually give rise to 125,000 new plants — a 50-per-cent efficiency in reproduction

TABLE 4. DETERMINATION OF THE PERCENTAGE OF GERMINATION OF FERTILE SEEDS

Head	Number of seeds	Number of seeds germinated	Number of seeds sterile	Percentage of germination
1	20	12	8	60 0
2	50	34	16	68 0
3	18	12	6	66 6
4	73	37	36	50 6
Total	161	95	66	
Average per cent germinated				60 5

TYPHA AS A COMMERCIAL ASSET

The vast areas of cat-tail have as yet been little utilized. The plant is rich in starch and other food values and grows in situations now regarded as waste lands. It would yield great quantities of supplies, if only a definite use for it could be found. The Indians and a few other races have used cat-tail products for various purposes. Hooker (1876) says:

The starchy rhizome of Typha possesses slightly astringent and diuretic properties, which led to its use in East Asia for the cure of dysentary, urethritis, and aphthae. The stems and leaves are used for thatching cottages. It has been vainly tried to utilize the bristles of the spike in the manufacture of a sort of velvet. [The pollen of Typha is made into bread by the natives of Scind and New Zealand.]

Engler and Prantl (1889) say: "The rhizome, rich in starch, may serve as food material; the leaves of several species are used for weaving. The pollen, which is easily recognized by the occasional tetrads, serves at times as surrogate for lycopodium powder."[2]

[2] Translation from the original German

Parker (1910) speaking of the plants used for food by the Indians, says: "The roots of the cat-tail were often used. Dried and pulverized the roots made a sweet white flour useful for bread or pudding. Bruised and boiled fresh, syrupy gluten was obtained in which corn meal pudding was mixed."

Mu-krats are very fond of the rhizomes of the cat-tail, and in the cat-tail swamps the muskrats are accordingly found in large numbers. The leaves of the cat-tail are used to some extent in the manufacture of barrels. On account of their spongy structure, the dried leaves, placed between the staves, expand greatly when moistened, thus making the barrels water-tight. The leaves are also used for chair bottoms. (Dudley, 1886).

The rich starch content of the plant is especially concentrated in the rhizomes, where the cells of the rhizome core (Plate XLV, 57 and 60) are completely filled with small starch granules. This is true of the rhizomes in their dormant or winter conditions (Plate XL, 13). If, however, one examines the cells later in the season, after the plant has attained a growth of several feet, the cells are found to be only partially filled with starch granules, much of the starch having been used up in the rapid early growth of the plant (Plate XL, 15). This fact, showing that they have a much greater concentration of starch during the dormant season than during the growing season, has a direct bearing upon the possible uses of the rhizomes, and any attempts made for the utilization of the starch should be made on the dormant rhizomes. The possibility of utilizing the Typha plant as a source of food has been discussed by the author in another paper (Claassen, 1919).

THE INSECT FAUNA OF TYPHA

The insects which are found on cat-tail have not hitherto been studied as a group. Most of them have been recorded as inhabiting cat-tail, but very little has been published on their detailed life histories and ecological interrelations.

The following discussion includes only those insects which have been found on cat-tail and studied during the course of this investigation. It includes six species of Lepidoptera, two of Coleoptera, eight of Hemiptera, five of parasitic Hymenoptera, and four of Diptera.

LEPIDOPTERA[3]

Arzama obliqua Walk.

Arzama obliqua Walk., a moth of the family Noctuidae, has been known in the adult stage for more than half a century. The species occurs throughout eastern United States and Canada, its host plant being *Typha latifolia*. In New York, near Ithaca, the writer has taken specimens from the following places: Michigan Hollow, Renwick Marsh, Bool's Back Water, McLean Bogs, Cascadilla Creek, and Ringwood Hollow.

Life history and habits

The life history of this insect is unusual and interesting from an ecological point of view. There is only one generation a year. The full-grown larva passes the winter in its burrow in the plant.

Egg-laying.— The eggs are laid on the surface of one of the first-formed leaves of *T. latifolia*, from six to fifteen inches below the tip. This later becomes one of the outer leaves of the plant. The eggs are placed on the leaf several layers deep. The lower layer covers the largest area and contains from twenty-five to forty eggs, while the upper layers cover only the central part of this bottom layer, forming a gradually sloping mass and containing from ten to twenty eggs in the two or more upper layers. The total number of eggs in one egg mass varies from thirty-five to sixty. The whole egg mass is covered with a thick layer composed of a mixture of froth, hairs, and scales from the body of the female. The egg mass greatly resembles a mass of spider's eggs (Plates XLI, 24 and 25, and XLVI, 65). It is of a dirty, yellowish-white color. It measures from twelve to fifteen millimeters in length, from seven to ten millimeters in width, and from three to four millimeters in height at the center. In shape it is oblong and convex, the edges gradually thinning out and adhering closely to the surface of the leaf. The long axis of the egg mass corresponds to the long axis of the leaf.

One female apparently lays several egg masses. In dissecting out the ovary of one female, 225 eggs were found, all fully formed and developed; and since only thirty-five to sixty eggs occur in a single mass, this indicates that one female may deposit about half a dozen egg masses.

[3] The Lepidoptera mentioned in this paper have all been determined by Dr. W. T. M. Forbes.

Usually only one egg mass occurs on the same leaf, but sometimes two, and in one instance three, masses were found on a single leaf. It is not uncommon to find two or three leaves of the same plant with an egg mass on each of them.

In the spring of 1918, careful observations were made for the appearance of the adults or the egg masses on the plants. In the laboratory, where moths had been bred, they failed to mate or to deposit eggs in the characteristic manner. A few females did lay infertile eggs on the stems and leaves of Typha. Egg masses were first noticed in the field on May 26. After this date new egg masses were constantly found until June 8. The height of egg-laying was between May 26 and June 2. At the McLean Bogs the egg masses appeared about six days later than those at the places around Ithaca.

The larva.— On turning the egg mass over, after the larvae have hatched, the empty egg shells are disclosed. The hatching process does not disturb the egg mass in the least. Without devouring the egg shell, the embryo breaks through it and bores directly into the leaf of the cat-tail, where it works as a leaf miner. This manner of hatching seems to be an excellent protective adaptation against egg parasites and other enemies. The mass is practically impervious to water. Thus from the time the egg is laid to the time when the larva hatches and enters the leaf to become a leaf miner, it is not once exposed to the direct dangers of enemies or of weather conditions.

Once the larvae enter the leaf, they begin their work as typical leaf miners. The structure of the leaf of the cat-tail plant is rather peculiar. The fibro-vascular bundles are found mainly in longitudinal, I-like partitions. This produces a loose inner structure with many large air spaces (Plate XL, 11). The longitudinal partitions are again traversed by transverse partitions which also are composed of parenchyma. A leaf of Typha with the epidermis removed to show this inner structure appears in Plate XLV, 58. When the larvae have entered the leaf, they begin to mine, mostly downward, scraping off the chlorophyll from the upper and lower epidermis of the leaf. They eat out the transverse partitions, leaving the longitudinal partitions and the fibro-vascular bundles undisturbed except when occasional larvae cut through to get in other channels. A few of the larvae may first mine upward toward the tip of the leaf, but soon they all proceed downward, moving abreast along the

channels. As many as eight larvae have been found together in one channel. It is probably due to such a crowded condition that a larva occasionally crosses over into another channel.

After the larvae have mined down for a distance of twenty to twenty-four inches, they molt in the mines and immediately afterward leave the mines through a little exit hole which is usually made on the inner side of the leaf. As soon as the larvae appear on the surface of the leaf they at once seek shelter, usually continuing down the stem of the plant and crawling behind the sheath of one of the outer leaves.

Since the larvae later become true stem borers, the question arises why they should come out of the mines of the leaf ten or fifteen inches away from the stem instead of remaining in the mines and working down the leaf until they reach the stem and can enter it directly. There are two plausible reasons against such behavior: first, the larvae later become solitary borers and after coming out of the leaf they separate and individually enter the stems of different plants; second, the width of the head of the second-instar larva exceeds the width of the average longitudinal channels in the external leaf. Careful measurements of the molted heads of the first-instar larvae and measurements of the width of the average channel of the leaf showed that the width of the head during the first instar was only slightly less than the width of the channel. The width of the heads of the second instar was considerably wider than the width of the channels of the leaf. Following are the average measurements:

Width of head of first-instar larva	0.597 millimeter
Width of head of second-instar larva	0.99 millimeter
Width of channel in leaf	0.62 to 0.72 millimeter

It would therefore be impossible for the larvae to remain in the leaf after the first molt unless they widened the leaf by taking out the longitudinal fibrous portions.

Although the larvae ultimately become solitary stem borers, they do not develop so later immediately after emergence from the mines and boreinward into the stem of the plant. In one instance, on June 20, 1916, it was found that a whole contingent of larvae had migrated to the head of the plant, where they found shelter behind the leaves that were sheathing the flower spike. Here they were feeding on the staminate flowers. A few days later they had all descended and scattered to different

plants. It is probable that such a migration to the flower spike was accidental, on the other hand, it may have been because the plant had a central stalk with a flowering spike that the larvae could not or would not enter it, for the writer has never found that they bored into a plant which had a flower stalk, nor has he ever found a plant in which the stem borers occurred producing a flower stalk.

The larvae enter the stalk from behind the sheath after they leave the leaf, and there they feed for some time. Only once were two larvae found in the same burrow. They normally become solitary borers, tunneling through the center of the stem, going downward to the crown, and sometimes even advancing for a short distance into the rhizome. This tunneling causes the central leaves of the plant to die, and consequently no flower spike is formed. The affected plants are easily recognized by the presence of the dead central leaves.

The larvae grow rapidly and by late fall have attained a length of nearly two inches. They leave the burrow full of the frass and the shreds of the fibrous tissue torn loose by their passage. In the fall, before the larvae go into hibernation, they eat out an exit hole in the stem, four to six inches above the ground, which they loosely plug up with frass and fibrous material. They then make a little compartment, or cell, by closing the burrow above and below with a mass of frass and fibrous material, as shown in Plate XLI, 27 and 28, and thus pass the winter. If one visits the marshes in winter and opens the plants, the larvae are found in the burrow, completely surrounded by ice. Larvae taken to the laboratory during September and October and placed in metal salve boxes on moist, sterilized sand, pupated in February and March. Adults emerged from sixteen to twenty days later. Larvae brought into the laboratory in the spring pupated much later, as is shown by table 5.

In the laboratory, several days before the larva transforms to the pupal stage, it begins to spin a thin, irregular layer of fine thread all over the surface of the sand in the salve box. In the field, one finds these loose webs lining the burrows in the stalks. The larva then becomes very sluggish and gradually shortens until it seems only about half of its normal length. The shiny, almost black, larval skin becomes much lighter in color. This is a sign that pupation will occur within twenty-four to

thirty-six hours. When the larva is ready to pupate, the larval head splits along the epicranial suture and the skin breaks open on the median dorsal line, along the first two thoracic segments, extending also about three-fourths of the way across the third thoracic segment. Gradually the skin slips off backward until the newly formed pupa is free. The pupa is at first entirely white except the cremaster, which is dark brown.

TABLE 5. LENGTH OF PUPAL PERIOD OF ARZAMA OBLIQUA

Specimen	Date of pupation	Date of emergence	Sex	Length of pupal stage (days)
1	February 21	March 11	Female	18
2	March 4	March 22	Male	18
3	March 10	March 29	Female	19
4	March 21	April 7	Male	17
5	March 25	April 11	Female	17
6	March 25	April 12	Female	18
7	March 25	April 11	Female	17
8	March 26	April 12	Female	17
9	March 28	April 14	Female	17
10	March 29	April 14	Male	16
Average length of pupal stage				17.6

TABLE 6. MEASUREMENTS OF PUPAE OF ARZAMA OBLIQUA*

Specimen	Females		Male	
	Length (millimeters)	Width (millimeters)	Length (millimeters)	Width (millimeters)
1	33.0	7.0	29.0	7.0
2	35.0	8.5	28.5	6.5
3	31.5	6.5	28.0	6.5
4	30.5	7.5		
5	31.5	6.8		
6	35.5	8.0		
7	34.0	7.0		
Average	32.85	7.25	28.5	6.7

*The measurements of the pupae of *Arzama obliqua* were taken as follows: length, from anterior end to the tip of the cremaster; width, the greatest lateral width of the pupa.

The first color of the body appears on the dorsal surface of the meso- and metathorax and on the first and second abdominal segments. After about ten minutes more the entire abdomen begins to assume a reddish color, the thorax, head, and wings still remaining nearly white, however. The pulsation of the dorsal vessel is very noticeable at this time. At the end of another twelve minutes the color is darkest on the sixth, seventh, and eighth abdominal segments, being more pronounced on the dorsal surface. Twelve minutes later the head begins to show color. In another half hour the entire pupa, except the wings, has become a reddish brown in color. The wings, which remain white the longest, now begin to show a little color. Later the pupa turns very dark brown, almost black.

Description of the stages

The egg

Light yellowish in color, round, though somewhat flattened, with the micropyle on the upper side, away from the surface of the leaf (Plate XLI, 21). 1 to 1.2 mm. in diameter and 0.8 mm. in height. Sculpturing very fine but quite characteristic, micropyle represented by a small depression surrounded by a rosette of about twelve elongate cells. This surrounded in turn by two other rings of more or less elongate cells, a reticulation following, with cells more or less regularly hexagonal, and, finally, the outside cells slightly elongated transversely. Entire reticulate area around the micropyle covering about two-thirds of the upper surface of the egg. Remainder of egg sculptured with a number of small tubercles, some occurring in lines so as to suggest circumferential bands of tubercles.

The first-stage larva (Plate XLI, 29)

Length 1.43 mm., width 0.58 mm. across the head. Head light brown, labrum and eyes darker. General color white, with a median purplish stripe. Spiracles on the eighth abdominal segment very large and dorsally located, as in the full-grown larva. After larva has been feeding for a few days, general color yellowish green.

The full-grown larva (Plates XLI, 22, and XLVI, 66)

Length 50 to 60 mm., width 6 to 7 mm. General color shiny muddy black. Head very dark brown. Lower half of clypeus light yellow. Basal knobs of antennae light grayish yellow. Labrum light gray. Thoracic shield the same color as the head. A light median line along the length of the prothorax. Individual segments of the body darker posteriorly. A dark median line along the dorsal surface of the entire larva. Ventral surface of the larva much lighter, being whitish gray in color.

The larva appears very much like a typical noctuid larva except for the position of the spiracles of the eighth abdominal segment. The spiracles on the other segments of the body occur in the natural place,

but the spiracles of the eighth segment have migrated from the lateral margin to a position on the posterior margin of the dorsal surface, as shown in Plate XLI, 30. The ninth abdominal segment consequently is much smaller, being only about half as thick dorso-ventrally as the other segments. This better adapts the larva to live in its burrow in a plant where an excess of moisture occurs. It is not at all uncommon to find a larva entirely submerged in the water with the exception of these large spiracles, which protrude above the surface of the water. These two spiracles are more than twice as large as the other abdominal spiracles.

The arrangement of the tracheal system in the larva is shown in Plate XLI, 31. It consists of two main longitudinal tubes, which originate from the spiracles of the eighth abdominal segment and extend as far forward as the first thoracic segment, where they are united by a transverse trunk. From this transverse trunk arise the tracheal tubes of the head. Paired spiracles are present on the meso- and metathorax and on the first eight abdominal segments. All of these spiracles are functional except those of the metathorax, which are much reduced and seem almost vestigial. Each of the spiracles, except those on the eighth abdominal segment, are connected with the main tracheal trunk of the body by small tubes, the tubes on the metathoracic segment being reduced to mere threads. Most of the tracheal branches of the body take their origin from the longitudinal trunk, near its junctions with the spiracles. From the thoracic spiracles, only small, branching tubes originate. From the first abdominal spiracle a large tracheal tube originates from the tube joining the spiracles to the longitudinal trunk, and smaller branches spring from the trunk. Segments 2, 3, 4, 5, and 6 of the abdomen each have a pair of large tubes arising from the main trunk just above the spiracles. These tubes branch out into two parts, as shown in Plate XLI, 31. Segment 7 of the abdomen has a number of smaller branches, and segment 8 has a number of still smaller branches in front of the large spiracles.

The pupa (Plate XLI, 23)

Female, average length 32.5 mm., width 7.25 mm.; male, length 28.5 mm., width 6.7 mm. Head, thorax, and appendages black. Abdomen dark brown. Frontal prominence very weak. Wings extending back over two-thirds of the fourth abdominal segment. Prothorax about two-fifths of the length of the metathorax. Surface of the head and thorax rugose. Clypeo-labral suture very distinct. Labrum distinct, the labial palpi nearly twice as long as labrum. Maxillae extending to the posterior margin of

the third abdominal segment. Femur of prothoracic leg not visible. Prothoracic tibia and tarsi prominent, reaching down two-thirds the length of the maxillae. Mesothoracic legs extending to the tips of the maxillae. Metathoracic legs invisible. Antennae reaching almost to the tips of the maxillae. Segments 4, 5, and 6 of the abdomen crossed dorsally by a transverse line of tubercles, the surface in front of the ridge coarsely punctate, but the part of the segment caudad of the ridge very finely punctate. On the ventral surface these transverse ridges occurring on segments 5, 6, and 7. Cremaster about as wide as it is long, somewhat flattened dorso-ventrally, very rugose, and bearing four short setae of equal length, spurs on the eighth abdominal segment dorsad. Female with two genital orifices. The peculiar sculpturing of the larva carried over and showing somewhat in the pupa.

The adult (Plate XLI, 26)

Length of body of female, 26 mm. Expanse of wings 54 mm. The original description by Walker (1865, 138) is as follows:

Cinereous brown. Antennae moderately pectinated in the male, slightly pectinated in the female. Femora and tibiae fringed, spurs moderately long. Fore wings with a dark brown oblique stripe, which extends from the base of the interior border to the tip of the wing, and is very diffuse on the outer side; an oblique fascia from the costa across the disk; another ringlet of like shape and hue, longitudinal, nearer the base, and shorter than the first and often obsolete; two submarginal oblique lines of blackish. Hind wings with a black oblique spot on the disk beneath.

Nonagria oblonga Grote

Nonagria oblonga Grote, a moth which also belongs to the family Noctuidae, has been reported by various authors as boring in the stems of *Typha latifolia*. Walton (1908) has described to some extent the habits of the later larval stages and has figured the full-grown larva, the pupa, and the adult. The writer has found the species to be common on *Typha latifolia* near Lawrence, Kansas, and in the following places around Ithaca, New York: Vanushing Brook, Cascadilla Creek, Bool's Back Water, Renwick Marsh, and Michigan Hollow.

Life history and habits

Nonagria oblonga Grote apparently produces only one generation a year.

Egg-laying.—The writer has been unable to find the eggs of this species, although the work of the larvae, from the first instar on, has been observed for three seasons, two seasons around Ithaca and one season in Kansas. The young larvae may be found just as soon as the cat-tail leaves appear above the surface of the ground. In Kansas, on April 20, 1917, when the leaves of the cat-tail were not more than four inches above the surface of the ground, the larvae were found at work in the tips of the leaves.

Although the larvae had evidently just started their work, and more larvae continued to appear during the following days, no eggs could be found on the plants. Again, in Ithaca, on May 20, 1918, first-instar larvae were discovered at work in the tips of the leaves, but no trace of the eggs could be discovered. This suggests the possibility that the females deposit their eggs in the fall on some of the old plants or other objects in the field, and that the species overwinters in the egg stage.

The larva.— The larvae enter the leaf of the cat-tail near the tip and at once begin to work as leaf miners. In their mining they do not restrict their work to the longitudinal channels, as do the larvae of *Arzama obliqua*, but they zigzag back and forth in the leaf, cutting through both the longitudinal and the transverse partitions. They feed on the chlorophyll and on the spongy parenchyma of the plant. The larvae are strictly solitary in their habits; only occasionally do two, or sometimes three, larvae occur in the same mine or even in the same leaf. The characteristic mine produced by the larva is shown in Plate XLII, 37. It is easily distinguished from the mine made by *Arzama obliqua*.

When the larvae are ready for the first molt, they suddenly widen their mine to the outer margins of the leaf, thus producing a narrow transverse mine extending nearly the entire width of the leaf but not severing it completely. This causes the leaf to wither from this point outward to the tip. In this withered part of the leaf the larvae molt, after which they mine downward through the lower, uninjured part. It seems that the natural condition of the leaf, which is very moist, is unfavorable to the molting of these larvae, and it is in order to overcome this excess of moisture that they sever the conducting tissues, thus causing the leaf to dry quickly. In this manner they obtain the required dryness in which to shed their first coat. This allows the larvae to remain under cover, where they are more protected than they would be in the open. The characteristic appearance of such a leaf and the cast skin of one larva in the severed part of the leaf, just above the transverse cut, are shown in Plate XLII, 37.

The larvae of this species do not cease mining after their first molt, and come out of the leaf, as do the larvae of *Arzama obliqua*, but continue as miners in the leaf for some time, often remaining in the leaf through the second, and even through part of the third, instar. Then, however, the larvae crawl away from the upper part of the leaf and seek protection

behind the sheath of the outer leaf, where they feed for a time before they enter the stem and become true stem borers. If the larvae emerge from the leaf soon after the first molt, they usually go down to the sheath of one of the first-formed leaves and there mine in the sheath for some time before entering the stem. Occasionally they feed for a while between two contiguous leaves. The effect of *Nonagria oblonga* Grote is easily recognized on the plant, since the work of the first-instar larva always causes the leaf at first to bend over and wither, and later, after the severed portion has become dry, to break off and fall to the ground. The leaf thus broken at the end, and the presence of the mine, are indicative of the work of these larvae. The writer once found a plant in which five leaves had been cut off by these larvae (Plate XLII, 36).

On entering the stem, the larvae work toward the center, where their borings materially hinder the further growth and development of the plant (Plate XLVII, 70). The presence of the larvae in the stems is indicated by the dried and withered central leaves of the leaf bundle. A plant so affected never heads, because the larva keeps the center tunneled out. The habits of the later larval stages of *N. oblonga* and *Arzama obliqua*, and their effect on the plant, are very similar.

Walton (1908) says of the habits of the larvae: "From all appearances the larva feeds for a time on the sheath of the stem, . . . As it increases in size it bores directly into the succulent central shoot, where it afterward remains until emerging as a mature insect."

When the larvae become full-grown, they transform to the pupal stage in the burrow of the plant. The larva lies with its head upward in the burrow. The exit hole is from two to four inches above the pupa and is carefully plugged up with a combination of frass and plant fibers.

Bird (1902) states that Nonagria has an extremely short pupal stage, from seven to nine days being the record of one brood.

At Ithaca, New York, the writer first found pupae on August 2, 1916. In Kansas the insects mature much earlier. There one larva pupated on June 24, 1917, and emerged on July 5, 1917, the pupal stage covering only eleven days.

The adult.—Around Ithaca the first adults were noticed on August 8, 1916, while in Kansas they were beginning to emerge by the 30th of June. Whether there is a second generation, especially in Kansas where the adults emerge so early, the writer has not been able to ascertain. The

adults failed to mate and lay eggs in captivity. However, no larvae were observed at work on the cat-tails later in the season. Therefore it is likely that if there is a later generation, it occurs on another plant

Description of the stages

The larva — The color markings of the larvae (Plate XLVII, 67) vary somewhat in different individuals, but mainly only in the degree of intensity of the colors. They may be described as follows:

General ground color light brown with a slight tinge of flesh color. Head light brown, mottled or speckled with darker brown. Epicranial suture, mandibles, and area just above the clypeus at lateral, darker brown. Six longitudinal, flesh-colored to brownish stripes along the entire length of the body. On each side of the median dorsal line two broad stripes and lateral to these stripes a narrow stripe, located on the lateral margin of the body. Above the spiracles another broad stripe. Below the spiracles, often, another more or less broken line, especially so in the young larvae. Prothoracic shield light brown. At the base of the last pair of the body a dark brown spot. Dorsal surface of the last abdominal segment light brown, with a few darker spots. Ventral side of the body of a light yellowish color. Length of fully grown larvae, from 40 to 50 mm.; width, from 4.5 to 5 mm. Larva cylindrical in shape and not unlike in form. Patterned as the larva of *Arzama obliqua*.

The pupa — Plates XLII, 33, and XLVII, 71.

Average length 27 mm.; width 7 mm. Color reddish brown, with head, thorax, and cremaster darker brown. Head with a conical projection about 2 mm. long. Wings extending to and over three-fourths of the fourth abdominal segment. Prothorax half as long as the mesothorax. Surfaces of the head and thorax nearly smooth. Anterior margin of labrum rounded. Labial palpi about two and one-half times as long as the labrum. Maxillae extending about one-sixth of the distance along the fourth abdominal segment. Maxillary palpi present as small triangular pieces. Prothoracic femur visible. Prothoracic legs extending to the length of the maxillae. Mesothoracic legs reaching a little beyond the tips of the wing cases. Antennae reaching a point half way between the tips of the mesothoracic wings and the tips of the maxillae. Metathoracic tarsi visible. Abdominal segments 2 to 7, inclusive, dorsally roughened with tubercles, especially prominent on segments 5, 6, and 7. Cremaster somewhat bilobed, with a rough margin, bearing four straight setae, two originating underneath, and the other two originating above, laterad to the median line. All these setae equidistant from each other, the middle one being longer than the outer ones.

The adult — The adult (Plate XLVII, 68) is of a pale reddish or yellowish color, measuring about 35 millimeters across the extended wings. The original description of the adult, as found in Grote (1882), is as follows:

Male. Pale reddish or yellowish gray, *something the color of Mythimna, P. oleaginea, Coen.* Primaries somewhat oblong, internal angle rounded away; apices subfalcated, costa

a little arched. Eyes naked. Clypeus mucronate. Palpi prominent, concolorous. Markings obsolete. The fine dark linear denticulate t. p. line barely discernable. Stigmata very small, indicated by paler shades. Hind wings with a faint mesial black shade band; centrally tinged with blackish, fringe and external edge like abdomen and very little paler than the rest of the insect. Beneath pale, with the disk of fore wings blackish; a common blackish extra-mesial shaded line. Minute black discal points. Smaller than *Typhae*.

Arsilonche albovenosa Goeze

Arsilonche albovenosa Goeze is another member of the family Noctuidae. It is found in Canada and in the northern, eastern, and central parts of the United States. It is a general feeder and has been reported on willow, smartweed, buttonbush, grass, and other plants. *Typha latifolia*, the writer believes, is here reported for the first time as a food plant of this species.

Life history and habits

This moth is reported to have two generations a year. The writer, however, has followed it through only one generation at Ithaca, where two adults emerged on August 15.

Eggs and egg laying. The eggs are deposited in long patches on the surface of the cat-tail leaf, usually ten to fifteen inches from the tip. The eggs overlap one another as shingles do. They lie on the leaf in rows, the number of rows varying from three to seven, and the rows overlapping one another as well as the individual eggs in each row. The number of eggs in one patch ranges from 60 to 161.

As the egg develops, it becomes much darker, turning very dark just before the larva emerges.

The larva. Immediately after hatching, the larva devours the empty shell and then begins to feed on the surface of the Typha leaf, where it scrapes off the chlorophyll. As the larva grows and feeds more voraciously, it usually migrates to the end of the leaf, where it eats off the tip of the leaf or devours chunks out of the edge of the leaf, as shown in Plate XLVI, 62.

When the larva has attained its full growth, it ties two cat-tail leaves together, and between them spins a tough cocoon in which it pupates. Two larvæ pupated in the laboratory, under the author's observation, on July 23, 1916, and two others on July 25, 1916. The former both emerged on August 15, 1916. This apparently indicates the length of the pupal stage to be nineteen days.

Description of the stages

The egg (Plate XLVI, 61)

Flat; saucer-like or shell-like in shape, and grayish white in color. Diameter, as seen from the top, varying from 0.89 to 1 mm., thickness of egg about 0.2. Sculpturing very pretty, micropyle in center of dorsal surface consisting of a dot with a rosette of elongate cells around it. Radiating from the rosette to the margin of the egg, about 45 small ridges, indented transversely by small, rounded depressions.

The larva.— The first-instar larva, within twenty-four hours after hatching, is described as follows:

Length 2 mm. Entire head jet black, thoracic shield dark brown; meso- and metathorax light gray with dark tubercles. Segments 1, 4, 5, and 8 of the abdomen dark brown with gray tubercles. The other segments of the abdomen light yellow with gray tubercles. From these gray tubercles originate long hairs.

Beutenmuller (1901) gives the following description of the full-grown larva (Plate XLVI, 62):

Head black, with an inverted V mark on the face, two white stripes on top, and mottled with white at the sides. Body black, two yellow lines on each side of the back and one on each side below the spiracles. The body is also mottled with confluent streaks, but less so on the dorsum. Warts orange with light and dark bristles, along the extreme sides a row of orange spots. Underside pale whitish. Length 40–45 mm.

The pupa (Plate XLVI, 63)

Length 18 mm., width, 5 mm. General color dark brown. Wings extending as far back as the fourth abdominal segment. Front of the head with two rounded, rugose ridges running up and down. Clypeo-labral suture very distinct. The front margin of the labrum rounded. Labial palpi three times as long as the undivided labium. Maxillae extending down to the beginning of the third abdominal segment. Prothoracic femur visible and the prothoracic tibia and tarsi extending down almost to the tips of the maxillae. Mesothoracic legs extending to the middle of the fourth abdominal segment. Antennae just failing to reach the tips of the mesothoracic legs. Metathoracic tarsi plainly visible. Ventral surfaces of segments 5, 6, and 7 finely granulate anteriorly, posteriorly finely punctate. The other segments smooth. On the dorsal surface, the metathorax and the first seven abdominal segments very roughly tuberculate. Cremaster broader than it is long and bearing from 40 to 50 short, straight spines.

The adult. — The adult (Plate XLVI, 64) is described as follows by Beutenmüller (1901): "Fore wings white, and more or less heavily marked with fawn brown streaks between the veins, giving the insect a very characteristic appearance. Hind wings and body white. Expanse, 34–45 mm."

Archips obsoletana Walk.

Archips obsoletana Walk. is a moth belonging to the family Tortricidae. This insect has been reported from the Atlantic states and from Illinois. The author has found it in Kansas and in New York. Slingerland (1901) suggested "the obsolete banded strawberry leaf-roller" as a common name for the insect. *Archips obsoletana* Walk., although it lives on various host plants, prefers those which grow in moist situations, and is here reported on *Typha latifolia*.

Life history and habits

The habits of this insect as a leaf-roller on strawberry have been studied rather carefully by Slingerland (1901). According to his report, there are three generations a year in New York. It is not known in what stage the insect passes the winter.

Egg-laying The eggs have not been observed in nature. In the laboratory, they were deposited in a large mass on the side of the glass cage.

The larvae The writer's observations on the habits of the larvae of this species have been restricted to those specimens found on *Typha latifolia*. The larvae and their work on cat-tail were first noticed on some cat-tail heads from Lawrence, Kansas, sent to the author by Dr. H. B. Pinngerford and received at Ithaca on July 17, 1916. A number of the heads showed the effects of the work of the larvae of *Archips obsoletana*. On August 12, 1916, larvae of this species were also found at work on the heads of cat-tail plants in the McLean Bogs. One pupa was also discovered at this time.

The larva works on the immature heads of the cat-tail, feeding on the tender styles of the pistillate flowers and sometimes eating off the tops of the developing ovules (Plate XLVII, 69 and 72). The stigmas are not eaten, instead they are lined underneath with a thin, but closely woven, layer of silk. This silk layer, together with the stigmas on top, forms a protective covering over the larva. When this covering is torn loose, the larva quickly repairs it.

In the laboratory, the larvae at times left the heads and fed on the leaves of the cat-tail; but they always provided themselves with a protected place, either by tying two leaves together or by spinning a silken tube between a leaf and the side of the glass cage. In this tube the larva remained, never leaving it entirely but always keeping the tip of the

abdomen covered and protruding the head to feed. As the larva fed downward, it lengthened this silken tube. In the field, the author has not observed the larvae feeding anywhere on the plant except on the head.

When the larva becomes full-grown, it goes to the top of the head, to which it then ties a leaf in order to form a place in which to spin its cocoon for pupation. The silk used to tie the leaf to the head is covered with a mixture of frass and the remains of the staminate flowers. If a leaf is not within reach of the larva, the cocoon is made on top of the head, near the rachis, and covered with the remains of the staminate flowers. After pupation, the wind and rain soon tear off the covering made by the larva and the head has then the appearance of having been shaved in patches. Plate XLVII, 73.

Description of the stages.

The egg. — Slingerland (1901) describes the egg somewhat as follows:

Thin oval, light brown to yellow, overlapping each other not unlike the shingles of a house. Shell is finely reticulated, the micropyle showing plainly at one end.

The larva. — The larva may be described as follows:

Olive green, with a light brown head and thoracic shield, both marked with black; the body sparsely hairy. Each light-colored hair arising from pale, roughened tubercles. The newly hatched larva very light yellow, with a brown head. Length of full-grown larva about 17 mm. Plate XLVII, 76.

The pupa. — The pupa is shown in Plate XLVII, 74. The following description applies to the female:

Length, including proboscis, 12 mm.; width, measured across the wings, 3.8 mm. General color reddish brown, the wings being somewhat lighter colored than the rest of the body. Wings reaching back as far as the middle of the fourth abdominal segment. Thorax region much enlarged, the appendages forming a distinct salient. Front of the head with an inverted Y ridge, as viewed from the cephalic aspect. A transverse ridge at the base of this Y. Clypeus and labrum prominent, and the clypeo-labral suture distinct. Eyes on clearly visible. Labial palpi one-fourth as long as maxillae. Maxillae extending halfway to the tips of the wings. Maxillary palpi elongate and triangular, reaching to the pro-lateral angles of the maxillae. Coxae of mesothoracic legs visible below the maxillae and the humeral. Femur and tibia of prothoracic legs large. Mesothoracic legs extending beyond the tips of the antennae. Antennae shorter than the wings by 0.8 mm. Metathoracic tarsi visible beyond the tips of mesothoracic leg and antennae. Genital orifice double. Cremaster slender, tapering, longer than it is broad, and bearing eight stout, curved setae, four extending from the apex and two on each side. Setae of body long and prominent on the dorsal surface, the first abdominal segment smooth. Segments 2 to 8, inclusive, each having two

transverse rows of strong spines, most prominent on segments 4, 5, 6, and 7. A few spines present on the ninth abdominal segment.

The adult.—The following description of the adult (Plate XLVII, 7) is quoted from Slingerland (1901):

General color varies from a wood-brown through cinnamon to russet, the hind wings and all four wings beneath are of a lighter yellowish-brown color. Many fine, wavy, transverse, dark brown lines occur on the front wings, showing more distinctly on the male. A band extending obliquely across these wings is a broad, dark brown band, more or less obsolete on the middle, and there is a subapical spot of the same color on each front wing.

Lymnaecia phragmitella Staint.

Lymnaecia phragmitella Staint. is a little moth belonging to the family Tineidae. Without question, this is the most common and the most abundant of the insects infesting the cat-tail. In distribution it is world-wide. It is found in England, central and southern Europe, northern Africa, Australia, New Zealand, and the United States. Its host plants are *Typha latifolia* and *T. angustifolia*. The writer has invariably found that the majority of Typha plants in any patch are infested by this insect.

Life history and habits.

The larvae.—Regarding the larvae of this species, Scanton (1870) wrote:

It was on a boggy piece of ground where *T. latifolia* grows, and all the heads of the tiny white heads of that plant exhibited a curious, tattered and ravaged appearance. At the period of our observation (in autumn), we shall find these young larvae [illegible] down near at the circle eaten some to all larvae [illegible] or near the ground, so that we shall find the same larvae, nearly full fed, about the [illegible] of these larvae is rather broad and flat, of a yellowish white, with [illegible] not [illegible] to pronounce them the larvae of *Lymnaecia phragmitella*.

The larvae restrict their work to the head of the plant, except occasionally when they bore into the stem to hibernate (Plate XLII, 35). The young larvae feed on the tender styles of the pistillate flowers, but as these grow larger and become dry, the larvae move farther inward and eat the seeds of the plant. As cold weather approaches, they migrate still farther inward, and finally locate near the rachis of the flower spike, where they often eat away the basal part of the little stalks which bear the seeds. The larvae spin an abundance of silk with which they tie the down, or pappus, together, thus keeping it from being torn off or blown away.

The cat-tail heads which are infested by these larvae present a striking appearance. The silk spun by the larvae holds the downy material together and does not allow the seeds to escape, but the heads fluff out

greatly and become twice or three times their natural diameter. Two heads, one heavily infested with the larvae of *L. phragmitella*, and the other uninfested, are shown in Plate XLV, 59. This is the appearance of the heads in the fall. During the winter and spring the uninfested heads lose all their seeds so that only the rachis remains, but the infested heads retain their seeds in the fluffy condition just described till the following summer, when the heads finally drop to the ground. A field in which the majority of the heads are heavily infested is shown in Plate XLIX, 84. This photograph was taken in July, just about the time that the new heads were forming. In the old heads, as well as in the newly formed ones, these larvae were present.

The larvae overwinter in the half-grown stage in the head of the plant, the fluffy material of the fruiting spike being their protection.

In the latter part of May or early June the larvae attain their full growth. Then, in the midst of the downy material, the larvae spin their thin, tough, white cocoons and transform to the pupal stage. Many of the larvae, leaving the heads, go down and bore into the stem of the cat-tail plant, forming burrows which they line with silk; and there they pupate.

In the laboratory, larvae were placed in vials containing little bunches of seeds from the head of Typha. The larvae spun cocoons in the vials and pupated. Some of the larvae bored into the corks, lined the tunnels with a little silk, and then transformed.

The average pupal stage lasts 29.4 days. This was ascertained from data on five individuals in the laboratory, as shown in table 7. Cocoons

TABLE 7. DETERMINATION OF THE PUPATION PERIOD OF LYMNAECIA PHRAGMITELLA STAIN.

Specimen	Date of pupation	Date of emergence	Length of pupal period (days)
1	June 4	July 1	27
2	June 6		
3	May 30	July 1	32
4	May 31	July [illegible]	33
5	June 5	July [illegible]	31
6	June 4	June [illegible]	24
Average			29.4

and pupae, as they were removed from the pappus of the head of a Typha plant, are shown in Plate XLVIII, 82

The adult.— The first adults were observed to emerge in the laboratory on June 8, 1916, and the maximum emergence occurred between June 25 and June 30. In the spring of 1918, the moths first appeared in the laboratory on June 10. Immediately after emergence the adult moths often rest on the cat-tail heads, as shown in Plate XLIX, 85. Stainton 1870 speaks of the adult as follows:

If in July we visit a locality in which the *Typha latifolia* grows we may probably find towards evening some small grayish-ochreous moths, with the anterior wings rather streaked with brownish towards the apex, and with two dark brown spots ringed with white on the disc: these would no doubt be the perfect insects of *Laverna Phragmitella*.

Description of the stages

The larva (Plate XLII, 32)

Length from 10 to 12 mm., width 2.5 mm. General ground color yellowish white. Ventral side entirely white, with the exception of the brownish, chitinized legs and prolegs. Dorsal surface with 5 longitudinal brown stripes. The median stripe rather narrow, the next stripe, on each side of the median line, wide and somewhat lighter in color, the stripes on the lateral margin, above the spiracles, more or less broken into blotches. Head light yellow, blotched with brown. Preanal suture dark brown. Posterior part of the head dark brown. Mandibles and labrum dark. Prothorax mottled with dark brown. The last abdominal segment dotted with dark brown spots, as shown in Plate XLII, 32.

The pupa (Plate XLII, 34)

Length 9–10 mm., width 2.1–2.3 mm. General color yellowish brown. Head with a blunt, rounded projection. Wings reaching to the middle of the sixth abdominal segment. Front of elypeal suture faint. Labrum with outer margin rounded. Labium not visible. Maxillae broad at the base and much narrower at the proximal half. Maxillary palpi present as small triangular pieces. Prothoracic legs extending two-thirds the length of the maxillae. Mesothoracic legs not reaching quite to the tips of the maxillae. Antennae very slender, reaching the tips of the wings, and contiguous all the way to the tip. Metathoracic legs invisible. Rudimentary prolegs visible on the sixth segment. No definite sculpturing on the body. On the dorso-caudad surface of the last abdominal segment, eight hooked setae, arranged in groups of four. In each group three setae in a straight transverse line, but the fourth seta just cephalad to the middle one of the group. Cremaster undeveloped.

The adult. The length of the adult, with wings folded, is from 10 to 12 mm. Stainton (1870) gives the following description of the adult:

Head pale brownish-ochreous, face paler. . . Antennae pale grayish-ochreous, spotted with dark brown. . . Anterior wings pale brownish-ochreous, the costa beyond the

middle paler on the disc, nearly in the middle, is an elongate dark brown spot surrounded by white, and in a line with it at the end of the discoidal cell is another similar spot. A brownish streak frequently connects the two, and the entire apical portion of the wing is more or less streaked with brown. . . . Posterior wings pale gray, with grayish-ochreous ciliæ.

Dicymolomia julianalis Walk.

Dicymolomia julianalis Walk. is a member of the family Pyralidæ. It is found throughout the southern part of the United States. Ithaca is probably near its northern limit. Its host plant is *Typha latifolia*.

Life history and habits

Dicymolomia julianalis Walk. has but one generation a year. It passes the winter in the half-grown larval stage. The habits of this insect are very similar to those of *Lymnaecia phragmitella*.

Egg-laying. — The eggs of *D. julianalis* are placed in the heads of the cat-tail, being inserted singly in the down, or pappus, of the seed. They are fastened to the pappus at about the level of the kernel of the seed. The eggs were first found on July 25, 1918, at which time they were rather common. It was not at all difficult to locate them, once it had been discovered where to look for them. The period of egg-laying has not been carefully determined, but apparently there were no eggs laid before the middle of July and none after August 10. The eggs are placed in the heads of the cat-tail with the blunt, or anterior, end outward. Several eggs are shown in the cross section of a head of *Typha latifolia*, in Plate XLIII, 45.

On July 25, 1916, the writer watched one of these eggs hatch. The larva lay in the egg, stretched to its full length, and could be seen moving back and forth inside the egg shell. It ate its way through the egg shell and escaped (Plate XLIII, 46). When about half of its body was out of the shell, the larva gained a foothold on the pappus and pulled itself the rest of the way out of the shell. The larva does not devour the empty shell, but at once buries itself in the head of the plant, where it eats the tender styles of the pistillate flowers. The empty shell remains attached to the pappus. The time from the moment that the larva actually began to eat through the egg-shell till it was freed was about twenty-five minutes.

The larva. — *D. julianalis* spends its entire larval period in the head of the cat-tail, obtaining its food, first from the styles of the pistillate

flowers, and later from the seeds and the dried-up parts of the flower. As soon as hatched, the larva begins to feed on the styles, leaving the stigmas to form a sort of covering over itself. These severed stigmas are spun together with a little silk and thus held in place. The larval habits of both *Lymnaecia phragmitella* and *D. julianalis* are very similar in their early stages. As the cat-tail heads become more mature, and the larvae grow larger, they enter deeper into the head, and their presence is not so readily detected as when they are working near the outer surface where the little raised patches of fluffy material they produce are easily seen. The appearance of a head of Typha within a week after the larvae had hatched and entered the head is shown in Plate XLIX, 86. As in the case of *Lymnaecia phragmitella*, the seeds are kept from scattering, by being tied together with silk woven by the larva. Neither wind nor rain is able to tear apart the heads so protected. Accordingly they form a good shelter for the larvae during the winter. The larvae of *D. julianalis* bore into the axis of the flower spike and there spend the winter in the half or two-thirds-grown stage. The rachis, with the characteristic tunneling of the larvae, is shown in Plate XLIII, 42 and 43. These tunnels are later lined with a little silk and in them the larvae construct tightly-woven cocoons in which they transform to the pupal stage. Many of the larvae, however, remain in the fluffy material in the heads to spin their cocoons and pupate. Pupation begins about the first of June. The adults emerge during the latter part of June and the first part of July.

During the spring of 1916 the author did not find any dead larvae in the heads of the cat-tail; but in the spring of 1918 all the larvae of this species which he observed were dead, evidently having been killed by the severe cold of that winter. At that time even the larvae in tunnels of the axes of the heads were dead. This was not true of the larvae of *Lymnaecia phragmitella*, however.

Description of the stages

The egg

Elongate oval, tapering considerably toward the posterior end and rather blunt at the anterior end (Plate XLIII, 38). Very long in proportion to its width, measuring 1 mm in length and 0.39 mm at its greatest diameter. Color of egg white, with a slight blush tinge in refracted light. Sculpturing rather faint, consisting of fine, more or less hexagonal reticulations (Plate XLIII, 39, drawn with the camera lucida).

The larva.— The larva of the first instar is shown in Plate XLIII, 40. The following description is taken from a larva about thirty minutes after its emergence from the egg:

Length 1.19 mm., greatest width 0.28 mm. General color light pinkish or flesh color. Head and thoracic shield mottled with darker brown, restricted in the thoracic shield to the posterior part. A dark mottled area on the dorsal surface of the last abdominal segment also.

The full-grown larva (Plate XLIII, 41) is described thus:

Length from 7 to 10 mm.; about 2 mm. at its greatest width. Much flattened, and in general shape much like *Lymnaeca phraqmitella*. General color flesh color. No special markings on the body except, as in the first instar, on the dorsal surface of the first thoracic segment and on the last abdominal segment. Head dark brown, with darker blotches near the outer margin. Epicranial suture very dark brown. Prothoracic shield dark brown, slightly lighter than the head, with two oblique oval spots near the lateral margin, the shield being mottled near the posterior margin. Dorsal surface of the last abdominal segment mottled with brownish patches or spots, as shown in Plate XLIII, 41. Larva easily distinguished from that of *Lymnaeca phraqmitella* in that it does not possess the five longitudinal stripes on the dorsal surface of the body.

The pupa (Plate XLIII, 44)

Length 7.8 mm., width 2.9–3 mm. General color yellowish brown to dark brown. Front of head not visible from the ventral aspect. Clypeo-labral suture distinct. Labrum with an emargination and very small, appearing somewhat like an arrow head. Two long hairs on the clypeus. Wings extending two-thirds across the fourth abdominal segment. Maxillae extending to the wing tips. Maxillary palpi absent. Prothoracic femora visible. Prothoracic leg extending two-thirds the length of the maxillae. Mesothoracic legs reaching to the tips of the wings. Antennae reaching to a point halfway between the tip of the prothoracic leg and the tips of the maxillae. Metathoracic legs not visible. Cremaster subquadrate, nearly smooth, with six equally long, hooked spines arranged in groups of threes on the outer angle of the cremaster. Rudiments of prolegs on segments 5 and 6 of the abdomen. General surface of the body smooth.

The adult.— The adult female, shown in Plate XLVIII, 81, measures 6 mm. in length and has a wing expanse of 18 mm. Walker (1870) describes the adult as follows:

Whitish, slightly marked with ferruginous. . . Antennae stout, submoniliform. Abdomen with brownish speckles. . . Legs stout. . . Fore wings with two reddish bands: the first exterior, the second marginal, the intermediate part with blackish specks, which are somewhat confluent by the bands.

COLEOPTERA

Calendra pertinax Oliv.[1]

Calendra pertinax Oliv. is a beetle belonging to the family Calandridae. Blatchley and Leng (1916) state that *Calendra pertinax* "ranges from New England and Canada to Michigan and Utah, south to Florida." Satterthwait (1920) reports this species from the following states: Indiana, Missouri, Maryland, and New York. The author has collected and reared it in Lawrence, Kansas, and in Ithaca, New York. A variety of *pertinax*, called *typhae* Chittendon, has been reared from the roots of *Typha latifolia* in California. The known host plants of *C. pertinax* are *Typha latifolia*, *Acorus calamus*, corn (*Zea mays*), and *Sparganium* sp. The writer has found *C. pertinax* in *Typha latifolia* and in *Sparganium* sp.

Life history and habits

The weevil is found to be most abundant in Typha patches where the plants grow in sod or grassy soil. This has been found to be true in New York as well as in Kansas. In the wet, grassy places along the railroad tracks south of Ithaca, where Typha grows intermingled with various species of grasses, the larvae were found to be most numerous. In some of these patches nearly every plant was infested. However, the weevil was found also in the larger cat-tail patches of Renwick Marsh around the biological field station.

Egg-laying. The eggs are inserted into the outer sheath at the base of the plant, very near the surface of the ground. No females were actually observed in the act of ovipositing, but the newly laid eggs were always found with the end protruding from a little slit in the sheath (Plate XL, 17). In very wet places it is likely that the eggs are placed above the surface of the water, but the writer observed them only on cat-tails growing in a rather dry situation.

The period of egg-laying has not been fully determined. Eggs were first found in Kansas on June 28, 1917. At that time, however, first- and second-instar larvae also were found in the plants, so that egg-laying must have started some time before, probably as early as the latter part of May. Eggs were found in the stems as late as July 17, when the

[1] Determined by E. C. Van Dyke.

observations had to be discontinued. The period of egg-laying is therefore spread over a number of weeks.

The larva.— In the laboratory, the larvae were placed in tin salve boxes which had been partly filled with sterilized sand and moistened with boiled water. A little excavation was made at one end of a fresh piece of the rhizome of cat-tail, and in this the larva was placed and left to feed. Such pieces of rhizome, two or three inches long, remained fresh from three to five days. As the larva became older and needed more food, these pieces of rhizome had to be replaced more often. By splitting the piece open, excavating a little hole in the center for the larva, and then binding the pieces together again with rubber bands, observations could be made from day to day without unduly disturbing the larva.

As soon as the larvae are hatched, they begin to bore directly into the stem, working toward the center, and thence downward toward the crown, and from there into the central axis of the rhizome (Plate XL, 19). Like the other borers of the cat-tail, this larva at once seeks the central part of the plant, where the tissue is most tender and succulent. However, the weevils seem to have a special preference for starchy food, and for this reason they work downward to the rhizome, the core of which is composed mainly of starch (Plate XLV, 60). In rearing the larvae, it was found that they would not eat any other part of the rhizome except the starchy core. As many as seven larvae have been found in a single plant. In one instance they were all working at the crown and as a result had nearly cut off the plant.

The affected plants present a somewhat stunted appearance. Sometimes the central leaves die and the plant fails to head out. The tunneled rhizomes shrivel up considerably and often darken decidedly.

The larvae grow very rapidly, and the time from hatching to the pupal stage averages about three weeks. When the larva has become fully grown, it prepares an oblong pupal cell in the stalk of the plant, from one to three inches above the ground (Plate XLVIII, 80). The pupal cell is made of partly masticated pieces of the stalk, with which the burrow is plugged above and below. In the laboratory some of the larvae pupated in their burrows in the rhizome, while others, that were reared in plants growing in flower pots, tunneled through the soil to the bottom of the pot and there made a smooth, oblong, unlined, earthen cell in which they transformed. The reason for their going down into the soil appeared to be a

desire for a moist place in which to pupate. The plants in the pots had dried up completely, and the soil, too, was quite dry, so that in order to find a moist place the larvae were forced to go to the bottom of the pot.

The length of the pupal stage seems to vary considerably. Eight pupae were kept under observation, and the results are given in table 8:

TABLE 8. LENGTH OF PUPAL STAGE OF CALENDRA PERTINAX OLIV.*

Specimen	Date of pupation	Date of emergence	Length of stage (days)
1	July 15, 1917	July 24, 1917	9
2	July 15, 1917	July 22, 1917	7
3	July 19, 1917		Died
4	July 21, 1917	July 27, 1917	6
5	July 27, 1917		Put in preservative
6	July 26, 1917	August 8, 1917	13
7	July 29, 1917	August 11, 1917	13
8	July 29, 1917	August 11, 1917	13
Average			10.16

* Dates of emergence of first six pupae were determined for the writer by Dr. P. B. Lawson, of Lawrence, Kansas. The last two pupae were observed by the author himself.

Description of the stages

The egg (Plate XL, 16)

Average length 2.15 mm., average greatest width 0.85 mm. Elongate oval, scarcely subreniform-elliptical. Color almost pure white. No distinct marking or sculpturing. As the time of hatching approaches, turning yellowish, and becoming quite dark just before the larva emerges.

The larva (Plate XLVIII, 77)

Color dirty white. Head yellowish brown. Epicranial suture distinct. On each side of the epicranial suture a light line starting indistinctly at the vertex and running obliquely to the frontal suture. Mandibles very dark brown, almost black. Front of head darker near the fronto-clypeal suture. Clypeus light brown. Labrum with two curving sulci which divide it into three subequal parts. On the labrum four prominent hairs and a number of marginal hairs. Thoracic segment distinct. Prothorax with a yellowish, chitinized shield. Spiracles of prothorax large, oblong, and nearly twice as large as the other spiracles. Segments 4, 5, and 6 of the abdomen greatly enlarged. Spiracles located on the dorsal surface. Length of larva, in its curled-up position, about 13 mm., when straightened out, about 16–17 mm.; greatest diameter 7 mm.

The pupa.— The pupa is shown in Plate XLVIII, 79. The size of the pupae varies considerably. The average of the measurements of six pupae (table 9) showed the average length to be 14.2 millimeters and the width, taken across the prothorax, 5.76 millimeters.

TABLE 9.—MEASUREMENTS OF THE PUPA OF CALENDRA PERTINAX OLIV.

Specimen	Length millimeters	Width millimeters
1	15.8	7.0
2	13.2	5.2
3	12.5	4.8
4	15.4	6.3
5	14.8	5.8
6	13.5	5.5
Average	14.2	5.76

The pupa is large, naked, and dirty white in color. It may be described as follows:

From the dorsal view: Head almost or entirely concealed by the prothorax. Prothorax a little longer than the mesothorax and metathorax combined. Eight spines on the surface of the prothorax, arranged in pairs, to at the four corners of the subrectangular dorsum. Mesothorax terminating in a triangular lobe, without spines or setae. Metathorax with two prominent setae. On each of first six abdominal segments a transverse row of setae arranged as follows: segment 1, with a group of three setae on each side of the median line and one laterally just above the spiracle; segments 2 to 6, inclusive, with the same arrangement except that the groups lateral of the median line have four setae; segment 7 with one seta on the lateral margin; segment 8 with four spines, arranged in groups of twos on the posterior margin.

From the ventral view: Rostrum stout, reaching to the prothoracic tarsi. One pair of spines at the base of rostrum and another pair in line with the base of the antennae. Antennae elbowed and reaching almost to the tips of the femora. Each femur with a stout spine near the distal end. Wings reaching to the ends of the hind femora. On the eight abdominal segments, in each of the outer two apices, eight spines, arranged in groups of four.

The adult.— Blatchley and Leng (1916) describe the adult (Plate XLVIII, 78) as follows:

Elongate-oval. Black or reddish-black, shining, the interspaces of thorax and the alternate intervals of elytra covered with a dirty white coating. Beak as in key, three-fifths the length of the thorax, finely and sparsely punctate, foveate and finely grooved at least basally. Thorax longer than wide, foveate and finely constricted, vittae entire, the median one widest at middle, narrowed before and behind, lateral ones with edges sinuous, branched as described

above interspaces and sides of disc coarsely punctate. Elytra broadest at humeri, sides feebly converging to apical fourth, then more strongly to the rounded apex; striae with rather coarse, regular punctures, the broader and more convex intervals somewhat interrupted, minutely and sparsely punctate. Length 11–15 mm.

Notaris puncticollis Lec.[5]

According to Blatchley and Leng (1916), *Notaris puncticollis* Lec. (Plate XLVIII, 83) ranges from Newfoundland and Quebec to Minnesota and as far south as the Ohio River. The host plants reported for this species are cabbage, *Peltandra virginica*, and *Typha latifolia*. Webster (1893), writing of *Notaris puncticollis*, says:

In Wayne County, Ohio, a field of this swamp land was underdrained last year, and last January was plowed, no further cultivation being given it until late spring, when it was prepared and planted to cabbage, about 50,000 in number, set late in June. These have been attacked and many of them destroyed by the adults of two species of Rhynchophora (*Listroderes approximatus* Boh. and *Eriges puncticollis* Lec.). The former is supposed to be the chief depredator, though I myself saw the latter attacking the plants. First, great cavities are gouged out of the stems of the young plants, and later the base of the larger leaves are attacked from beneath. It is not unlikely that one and perhaps both of these species breed in Sagittaria, though I have some reasons for suspecting that the Eriges may breed in the common *Typha latifolia* or cat-tail.

On August 19, 1915, at the field station in Renwick Marsh, W. A. Hoffman found the adult of *Notaris puncticollis* Lec. in the burrow in the stem of Typha. The burrow appeared very much the same as that of *Calandra perlmar*. The writer, however, has not been able to find this species during the course of his studies.

HEMIPTERA

Ischnorhynchus resedae Panz.[6]

Ischnorhynchus resedae Panz. is an insect belonging to the family Lygaeidae. It is of general distribution, being reported from Europe, Asia, Central America, Mexico, Canada, and the United States. Among its host plants are included birch, conifer, heath, arbutus, *Typha latifolia*, and *T. angustifolia*. The two species of Typha are here reported for the first time.

Life history and habits

Egg-laying.—The eggs are laid in the spring, during May and June. They are deposited singly in the pappus of the old cat-tail heads of the

[5] Determined by C. W. Leng.
[6] Determined by Dr. H. H. Knight.

previous year. They are attached either to the seeds or to the pappus. When the egg hatches, the nymph either opens the cap or breaks through the egg shell, bursting it near the top.

The nymphs. — The various nymphal stages and the adults were first observed on the overwintering cat-tail heads in the summer of 1916. It was at first assumed that they were merely accidentally present on the cat-tail heads, but closer examination revealed that the bugs were feeding on the dry seeds of the heads.

The nymphs obtain their nourishment by thrusting the stylets of their beaks into the dry seeds (Plate XLIV, 53 and 55). During feeding, the long labium is often folded back under the body. In just what manner the bugs are able to extract nourishment from the dry seeds the author has not been able to determine. When crushed on the slide and examined under the microscope, the seeds show very little moisture. It is very probable that the insects secrete a fluid which dissolves or predigests the dry food material before it is taken into the body. The author has succeeded in rearing nymphs to the adult stage on these dry heads of cat-tail alone with no other food available. When placed on the green leaves of the cat-tail, the nymphs insert their beaks and feed. They are easily disturbed while feeding on the seeds in the laboratory. At the slightest provocation they rise up on their hind legs, quickly extract their stylets, and, by means of their front legs, stroke the stylets back into the labium. The labium is then folded into place and the nymph retreats to some sheltered place.

The adult — Adults were found mating in May and June. The female inserts her ovipositor into the male and copulation lasts from six to nine minutes. Mating is repeated a number of times at intervals of from five to ten minutes.

Description of the stages

The egg (Plate XLIV, 47)

Length 0.93 mm. to 1 mm., greatest diameter 0.29–0.30 mm. Egg elongate oval in shape, tapering considerably at the posterior end, and closed by a cap at the anterior end. This cap with a cone-shaped protuberance in the center and surrounded by a circle of hooked spines. The upper two-fifths of the egg finely reticulated; the lower three-fifths with longitudinal wavy and branching ridges. Color lemon yellow at first, turning bright red before the nymph emerges. Empty egg shell white. The egg closely resembling the seed of cat-tail, both possessing caps and very similar markings on the surface.

The first-stage nymph (Plate XLIV, 48)

Length 0.857 mm.; greatest width, across wing pads, 0.280 mm. Length of antenna 0.428 mm. When first emerging from the egg, the general color of the nymph bright red. Eyes carmine red. Abdomen, vertex of head, and lateral margins of the body, of a darker color than the rest of the body. Thorax, front of head, antennae, and legs, of a light yellowish color. Several hours after hatching, nymph of a different appearance: Head, thorax, and tip of the abdomen very dark red, almost brown. Abdomen carmine, mottled with yellow. Legs and antennae greenish yellow, the antennae lighter at the joints. The epicranial suture and the median dorsal thoracic line lighter in color.

The second-stage nymph (Plate XLIV, 51)

Length 1.5 mm., greatest width, across wing pads, 0.368 mm. Length of antenna 0.575 mm. General color carmine red. Head and thorax dark reddish brown. Intermixed with the red color of the abdomen, many yellowish blotches. Antennae dark red, lighter at the joints. Rostrum somewhat lighter than the rest of the head. Epicranial suture and median thoracic line pale. First thoracic segment uniformly dark, in the second segment the dark color restricted to two rectangular patches; in the third segment the darker color present in two transverse lines. The dorsal glands showing as short, brown, transverse lines between the abdominal segments 3 and 4, 4 and 5, and 5 and 6.

The third-stage nymph (Plate XLIV, 50)

Length 2.08 mm.; greatest width, across wing pads, 0.598 mm. Length of antennae 0.69 mm. General color a little darker than in the preceding stage. Head uniformly dark brown, except for the lighter epicranial suture and a lighter spot on the rostrum. Head and thorax covered with faint white pile. In this stage the pro- and mesothorax uniformly dark brown, with the dark patches on the metathorax a little wider than in the preceding stage. The light median line on the thorax present as in the previous stages. The mottled appearance of the red and yellow color of the abdomen more pronounced in this stage. Dorsal glands more plainly visible. Wing pads just beginning to show. Entire body more hairy than in preceding stages.

The fourth-stage nymph (Plate XLIV, 49)

Length 2.71 mm.; greatest width, across wing pads, 0.989 mm. Length of antennae 1.04 mm. Color of head and thorax dark brown. Epicranial suture and median dorsal line of thorax light red. Rostrum of head with a short black longitudinal line on each side. Eyes carmine red. Antennae slightly lighter than head and thorax, much lighter at the joints. Dorsum of prothorax on each side with a blackish, triangular, transverse spot, as shown in Plate XLIV, 49. Wing pads extending 5 mm. beyond the posterior margin of the mesothorax. The mottled color of the abdomen much as in the preceding stage. The white pile on the head and thorax thicker and more plainly visible than in preceding stages. Dorsal glands as in third stage.

The fifth-stage nymph (Plate XLIV, 54)

Length 3.35 mm.; greatest width, across wing pads, 1.61 mm. Length of antenna 1.38 mm. The general color similar to that of the previous stage, but the head and thorax now distinctly patterned. Epicranial suture as in previous stages. The part of the head back of the epicranial suture uniformly dark red. Rostrum yellowish with brown lines on each side, which meet behind the rostrum and then diverge outward until they join the brownish border inside the epicranial suture, thus producing on the head four yellowish patches separated by the brown lines in the shape of the letter X. Prothorax dark brown, punctate with circular yellow spots. From these spots, short white hairs arising. Transverse dark bands on the prothorax, as indicated in Plate XLIV, 54. Rest of thorax, including wing pads, dark brown. The surfaces of meso- and metathorax and the wing pads punctate with yellowish spots, less numerous than those on the prothorax, however. The bases of the wing pads indicated by light-colored, diagonal lines. The margin of the entire thorax and wing pads of a blackish brown color. Wing pads reaching to about the middle of the third abdominal segment. Abdomen colored much as in the preceding stage.

The adult Plate XLIV, 52)

Female, length 5.4 mm., greatest width, across the prothorax, 1.5 to 1.6 mm. Length of antenna 1.75 to 1.85 mm. General color dark brownish red. Posterior margin of head and area around eyes and ocelli black. Sides of rostrum black. Basal segment of antennae black, second and third segments of antennae yellowish brown with fuscous at the bases and apices, and the fourth segment dark red. Head and thorax thickly covered with dark punctures. Pronotum with two wavy transverse dark bands near the anterior margin. Corium pale yellowish brown with two black spots on the disk and four black spots on the inner lower margin. Legs reddish brown. Apical segments of tarsi black. Body covered with a very fine white pile. Male slightly smaller than female.

Siphocoryne nymphaeae Linn.[7]

Siphocoryne nymphaeae Linn., the reddish brown, plum aphis, is found in numbers on cat-tail during the spring and summer. This species also uses other water plants as its summer hosts, such as Nymphaea, Potamogeton, and others. The aphids are found on the surfaces of the leaves from the sheath out to the tip of the leaf. The writer observed this species on *Typha latifolia* at Ithaca in 1915, 1916, and 1918.

Aphis avenae Fab.[8]

The author found *Aphis avenae* Fab., the oat aphis, in large numbers, feeding on cat-tail, during the spring and summer of 1917, at Lawrence,

[7] Determined by Dr. Edith M. Patch.
[8] Determined by J. J. Davis.

Kansas. Frequently the young aphids were found behind the sheaths of the leaves, in the gelatinous material below the surface of the water in which the plants were growing.

Rhopalosiphum dianthi Schrank

Rhopalosiphum dianthi Schrank was reported on cat-tail by Sanborn (1906).

Rhopalosiphum persicae Sulz.

Rhopalosiphum persicae Sul. was reported on *Typha latifolia* and on *T. angustifolia* by Wilson and Vickery (1918).

Aphis gossypii Glov.

Aphis gossypii Glov. is found in small numbers on *Typha latifolia* during the spring and fall, according to Davidson (1917:65).

Macrosiphum granarium Kirby

Macrosiphum granarium Kirby, the grain aphis, is found in great numbers on Typha during the summer and fall, according to Davidson (1917:65).

Hyalopterus arundinis Fab.

Hyalopterus arundinis Fab., according to Davidson (1917:65), is found from April to June. The infestation on cat-tail is never large. There are four to ten generations. Aphids settle mainly on both sides of the blades, locating in colonies, usually not far from the tips.

HYMENOPTERA[9]

Five species of parasitic Hymenoptera were reared on insects which were found on cat-tails.

Aleiodes intermedius Cress

Aleiodes intermedius Cress was reared on larvae of *Arsilonche albovenosa*. On August 12, 1916, six specimens emerged from one larva.

[9] Det. by C. F. W. Muesebeck.

Apantales cinctiformis Vier.

Apantales cinctiformis Vier. was reared on larvae of *Nonagria oblonga*. A number of specimens emerged on August 8, 1916.

Elachertinae sp.

Five specimens of *Elachertinae* sp. were reared from a larva of *Lymnaecia phragmitella*. These emerged on June 15, 1916.

Pimpla indagatrix Walsh

On June 8, 1916, several specimens of *Pimpla indagatrix* Walsh emerged from the heads of cat-tails which had been kept in a covered jar in the laboratory.

Pimpla inquisitoriella D. T.

Several specimens of *Pimpla inquisitoriella* D. T. were reared from pupae of *Arsilonche albovenosa*.

DIPTERA[19]

The following flies were reared from cat-tail.

Platychirus quadratus Say

Platychirus quadratus Say was reared from the heads of cat-tail. The larvae were noticed in early spring in the overwintering cat-tail heads. Many adults emerged between May 21 and June 10.

Macrosargus clavis Will.

The larvae of *Macrosargus clavis* Will. live in the burrows made by the larvae of *Arzama obliqua* Walk. or of *Nonagria oblonga* Grote. They winter over in the larval stage, and the adults emerge in May and in early June.

Chaetopsis aenea Wied.

The larvae of *Chaetopsis aenea* Wied. also are found in the burrows of *Arzama obliqua* Walk. and of *Nonagria oblonga* Grote. Adults emerged on August 8.

[19] The first three species were determined by Dr. O. A. Johannsen, the last one by Dr. J. D. Tothill.

Sturmia nigrita Town.

Sturmia nigrita Town. is a parasite which was found living in the larva of *Arzama obliqua* Walk. In each of the two instances observed, there was only one parasitic larva present in each of the larvae of *Arzama obliqua*. Both dipterous larvae emerged from their host on March 25, 1918, through an opening which was made on the ventral side of the first thoracic segment. They pupated on the following day, and one adult emerged on April 9 and the other on April 10.

RÉSUMÉ

From an ecological point of view, the insect inhabitants of Typha may best be considered with respect to the part of the plant they affect. Accordingly they are thus classified in the following pages.

INSECT INHABITANTS OF THE HEAD OF TYPHA

The insects inhabiting the head of Typha include, among the Lepidoptera, *Lymnaecia phragmitella* Staint., *Dicymolomia julianalis* Walk., *Acleris obsoletana* Walk.; and among the Hemiptera, *Ischnorhynchus resedae* Panz.

The work of *L. phragmitella* and *D. julianalis* is very similar. Each has one generation a year. Their early larval habits are almost identical. They feed first on the tender styles of the pistillate flowers of the cat-tail plant, leaving the stigmas to form a covering over themselves. Later, they advance deeper into the head and feed on the seeds and other parts of the fruiting spike. Both overwinter in the half-grown larval stage. In the spring before pupation, however, their habits become somewhat different. Many of the larvae of *D. julianalis* bore into the rachis of the head, where they transform. The majority of the larvae of *L. phragmitella*, on the contrary, remain in the pappus of the cat-tail, where they pupate in closely woven cocoons. A few of the *L. phragmitella* larvae migrate down to the stalk of the plant, where they bore into the stems and transform. The adults of both species emerge at about the same time.

L. phragmitella is a species of world-wide distribution, while *D. julianalis* is generally restricted to the Southern States, though it is found as far north as New York. Of *L. phragmitella* the writer has found as many as 76 pupae in a single head, while of *D. julianalis* he has never observed more than six or eight individuals in one head.

Both of these insects are well adapted to live in the heads of cat-tail. Both spin an abundance of silk whereby they tie the pappus together and keep the head from being torn and the seeds from being scattered. This process of tying the pappus together assures the larvae of retaining their food supply and also furnishes them a protected and sheltered place for passing the winter. *D. juliannbs*, however, being a less hardy southern form, was unable to stand the severe temperature during the winter of 1917–18, and all the larvae found in the Typha heads that spring were dead.

Archips obsoletana should probably be classified as an incidental feeder on cat-tail. It is a typical leaf-roller, occurring chiefly on strawberry plants. However, once the larvae locate on the head of the cat-tail, they spend the entire larval period there and transform to the pupal stage on the plant. Since there are three generations a year, it is very probable that never more than one generation is passed on cat-tail, for these insects feed only on the tender styles of the pistillate flowers, and as these soon dry up, the later generations would not be able to find the tender food they relish. When living on the strawberry plant, these larvae roll themselves up in a leaf for protection. On the head of cat-tails they protect themselves by tying the stigmas together underneath with a lining of silk, thus forming a cover under which they live while feeding on the styles of the flowers. When placed in a cage with cat-tail leaves, the larvae prepare a covering for themselves by tying two leaves together and crawling between them. At the time of pupation they tie a leaf to the head of the plant and thus obtain the protection necessary during their transformation.

In the spring, the females of *Ischnorhynchus resedae* deposit their eggs in the old, downy heads of the cat-tail. The eggs closely resemble the seeds of cat-tail and thus are well protected from enemies. Immediately after hatching, the nymphs begin to feed on the seeds of the plant. They thrust their beaks into the dry seeds and apparently obtain their nourishment by injecting saliva into the seeds, which dissolves the solid material there so that they can suck it up into the body. The entire nymphal stage is spent in feeding on the dry seeds, a very remarkable and interesting adaptation. Due to the work of *L. phragmitella* and *D. juliannbs*, the seeds of many of the old heads are kept from being scattered by the winter storms, and *Ischnorhynchus resedae* simply takes advantage of these

conditions. It inserts its eggs into the pappus, where they are hidden from all enemies and where the nymphs find an abundance of food at hand which is not contested by any close relatives and which, indeed, is used by few other insects.

INSECT INHABITANTS OF THE LEAF OF TYPHA

The inhabitants of the leaf comprise two classes, the surface feeders and the leaf miners. The surface feeders include, among the Lepidoptera, *Arzama albocrnosa*, and among the Hemiptera, the Aphidae enumerated on page 501. The most common of the surface feeders is the noctuid caterpillar, *A. albocrnosa*. It is a general feeder but is very commonly found on cat-tail. The eggs are placed on the upper part of the leaf, and the larvae, as soon as hatched, feed on the leaf. A leaf thus infested has the appearance of having been skeletonized. After they grow larger, the larvae begin feeding on the edge of the leaf, where they eat out large sections.

The species of aphids mentioned on pages 500–501 may be classed as feeders on the leaf, although they occasionally feed lower down on the stem and sheaths of the plant.

The leaf miners include *Arzama obliqua* Walk. and *Nonagria oblonga* Grote. These two noctuid larvae do not restrict themselves entirely to leaf mining but they begin their larval life as leaf miners, later becoming true stem borers. Although the two species are related, their habits differ greatly. *A. obliqua* overwinters as a larva in its burrow in the cat-tail plant, whereas *N. oblonga* apparently passes the winter in the egg stage. The eggs of *A. obliqua* are laid in the spring, while those of *N. oblonga* are apparently laid in the fall. The young larvae of *A. obliqua* burrow gregariously, but the larvae of *N. oblonga* are solitary miners. The nature of their mines, too, is very different. *A. obliqua* advances down the channels of the leaf, leaving the longitudinal partitions of the leaf intact and only destroying the cross partitions, while *N. oblonga* produces a sort of blotch mine by zigzagging back and forth in the leaf and destroying both the longitudinal and the transverse partitions. Both species feed mainly on the chlorophyll of the leaf. When ready for the first molt, *A. obliqua* sheds its skin at once, right in the mine, near the healthy, undisturbed, succulent tissue of the leaf, but *N. oblonga*, when ready for the first molt, first severs the connecting tissue of the leaf in order to

produce a drier situation in which to cast off its coat. This variation indicates that *A. obliqua* is better adapted than *N. oblonga* to live in moist or wet situations. A comparison of the tracheal systems of the two larvae shows this yet more clearly. *A. obliqua* has the spiracles of the eighth abdominal segment located on the dorsal surface and they are more than twice the size of the other spiracles of the body. Directly attached to these spiracles are the two longitudinal tracheal trunks of the body. Segment 9 of the abdomen is flattened dorsally so as to be only half as thick dorso-ventrally as the other abdominal segments, thus making room for the large spiracles on the eighth segment. This allows the body of the larva to be almost entirely submerged in the water, for as long as these spiracles remain above the surface it suffers no harm. The tracheal system of *N. oblonga* has not undergone any such modifications, however. The spiracles on its eighth abdominal segment are located in the natural position and are the same size as the other abdominal spiracles. Consequently the larva is likely to suffer harm if much water gathers in the burrow, as often occurs in wet situations. The larvae of *A. obliqua* remain in the leaf of Typha only through the first instar, while the larvae of *N. oblonga* often remain in the leaf through the second and even the third instar. The nature of their mining habits may have much to do with the difference. *A. obliqua* does not destroy the longitudinal partitions of the cat-tail leaf, and consequently must get out after its first molt on account of its increased size in the second stage. *N. oblonga*, however, eats through the partitions in any direction and so is able to remain in the leaf for a longer period. After leaving the leaf, both larvae become solitary borers in the stalks of cat-tail.

INSECT INHABITANTS OF THE STALK OF TYPHA

The insects which work in the stalks of the cat-tail include two species of the Lepidoptera, *Arzama obliqua* Walk. and *Nonagria oblonga* Grote, and the Coleoptera, *Calandra pertinax* Oliv. and *Notaris punctiventris* Lec.

After the larvae of *A. obliqua* and *N. oblonga* leave the mine of the leaf, they become stem borers. Their methods of entering the stem are very similar. Both are frequently found feeding for a time between the sheaths of the outer leaves of the plant. From the sheath they either bore directly into the stem or enter from between the leaves at the leaf bundle. Both work their way to the center of the plant and excavate at

the point where the tender new tissue is forming. The effect of their work on the plant is very similar: the central leaves of the leaf bundle die and the plant fails to produce a fruiting stalk.

C. pertinax, the weevil, begins its larval life as a stem borer, later becoming a borer in the rhizome of the plant. The eggs of *C. pertinax* are inserted into the sheaths of the plant, near the ground. The newly hatched larvae bore to the center of the stalk and hollow it out just above the crown, thus arresting the further growth of the plant. After feeding on the tender tissue at the center of the stem for some time, the larvae enter the rhizome and there feed on the more substantial starchy food. When full-grown, the larvae return to the stalk and there form a pupal chamber in which the transformation takes place. There is only one generation. The larvae are ordinarily solitary borers, although as many as seven larvae have been found in one plant.

INSECT INHABITANTS OF THE RHIZOME OF TYPHA

The inhabitants of the rhizome are the Coleoptera, *Calendra pertinax* Ohv. and probably *Notaris puncticollis* Lec. The larvae of *C. pertinax* feed during the major part of their larval period on the starchy core in the rhizome of the plant. By first tunneling out the center of the stalk at the crown of the plant, they prevent the formation of new leaves, and in this way the larvae cause the starch to remain in the rhizome for their nutriment which would otherwise be used up in the growth of the plant. The leaves already formed are left undisturbed to manufacture and send down more starch to the rhizome. Very likely the habits of *N. puncticollis* are similar to those of *C. pertinax*.

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PLATE XXXIX

TYPHA LATIFOLIA

1, Sterile seed, showing large size of pericarp. 2, Fertile seed. (The pericarp fits closely over the kernel.) 3, Seed, or kernel, removed from pericarp. 4, Embryo protruding through pericarp. 5, Same as 4, with pericarp removed. 6, Growing embryo as it appears when removed from seed. 7, Embryo pushing open cap of seed. 8, Beginning of formation of root. (The arrow indicates the developing leaf.) 9, Further development of young plant. (The leaf has protruded and root hairs have developed on the root.) 10, Young plant with three leaves and three roots, showing disintegration of tip of first leaf, where it frees itself from the seed.

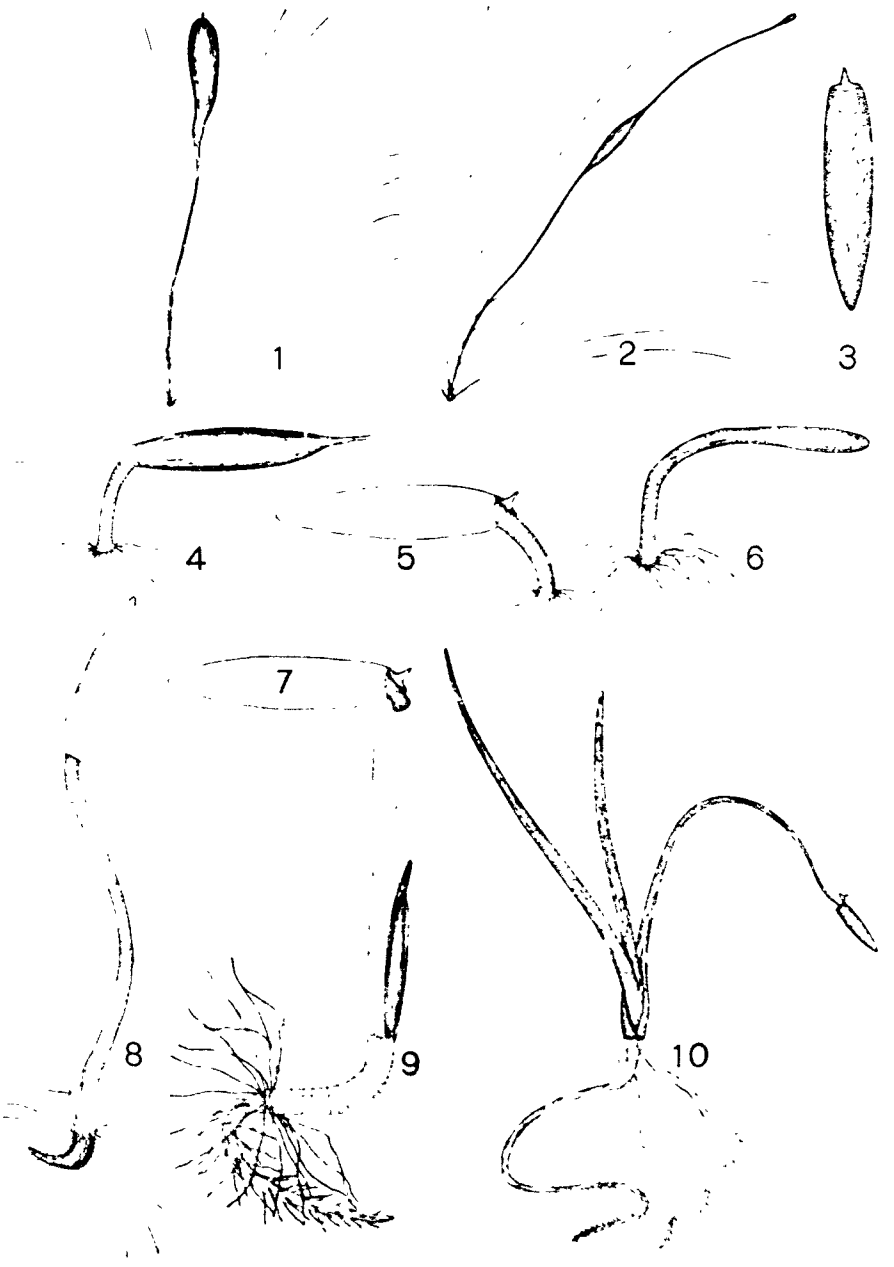
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PLATE XL

TYPHA LATIFOLIA AND CALENDRA PERTINAX

Typha latifolia.—11, Cross section of leaf.—12, Cross section of a small part of leaf, showing more detail.—13, Cells of rhizome filled with starch grains. (Dormant season.)—14, Part of 12 enlarged to show structure of epidermis, chlorophyll, supporting tissue and vascular bundles.—15, Cells of rhizome partly filled with starch grains. (Growing season.)—18, New offsets.

Calendra pertinax.—16, Egg.—17, Egg inserted in sheath of cat-tail.—19, Rhizome of cat-tail cut open to show larval work.—20, Newly hatched larva.

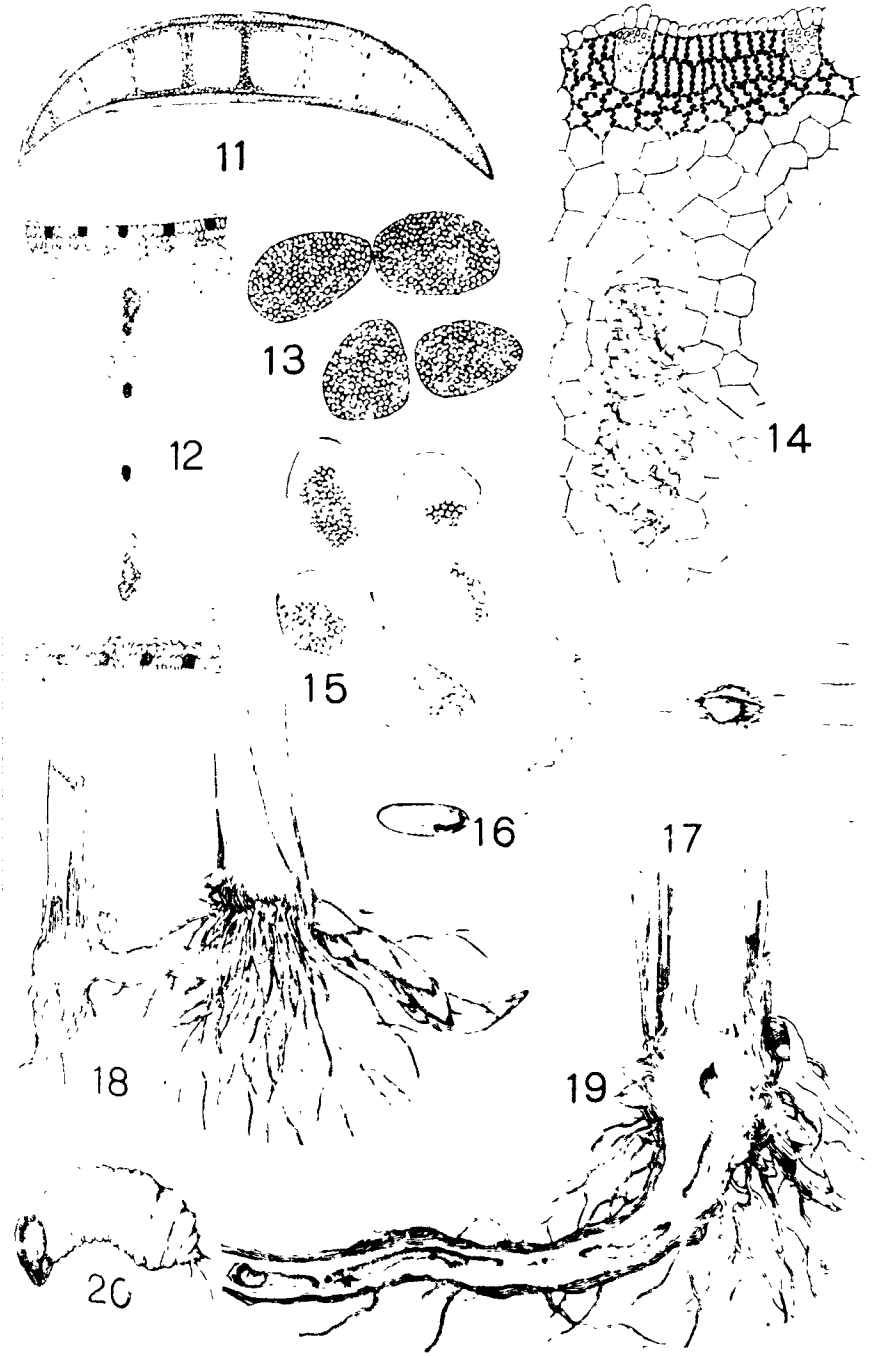
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PLATE XLI

ARZAMA OCTOTA

21, Egg. 22, Full-grown larva. 23, Pupa. 24, Egg mass on cat-tail leaf. 25, Larva boring in cat-tail leaf, showing the mode of entering the leaf, thus causing the [illegible] 26, Cat-tail leaf with egg mass, showing [illegible] and exit holes of larvae. [illegible] 27 and 28, Full-grown larvae boring in stalks of cat-tail. 29, [illegible] larva. 30, Dorsal aspect of [illegible] segments of larva, showing position of spiracles on [illegible] segment. 31, Tracheal system of full-grown larva. Only the first one of the [illegible] tracheal tubes is shown in its entire length.

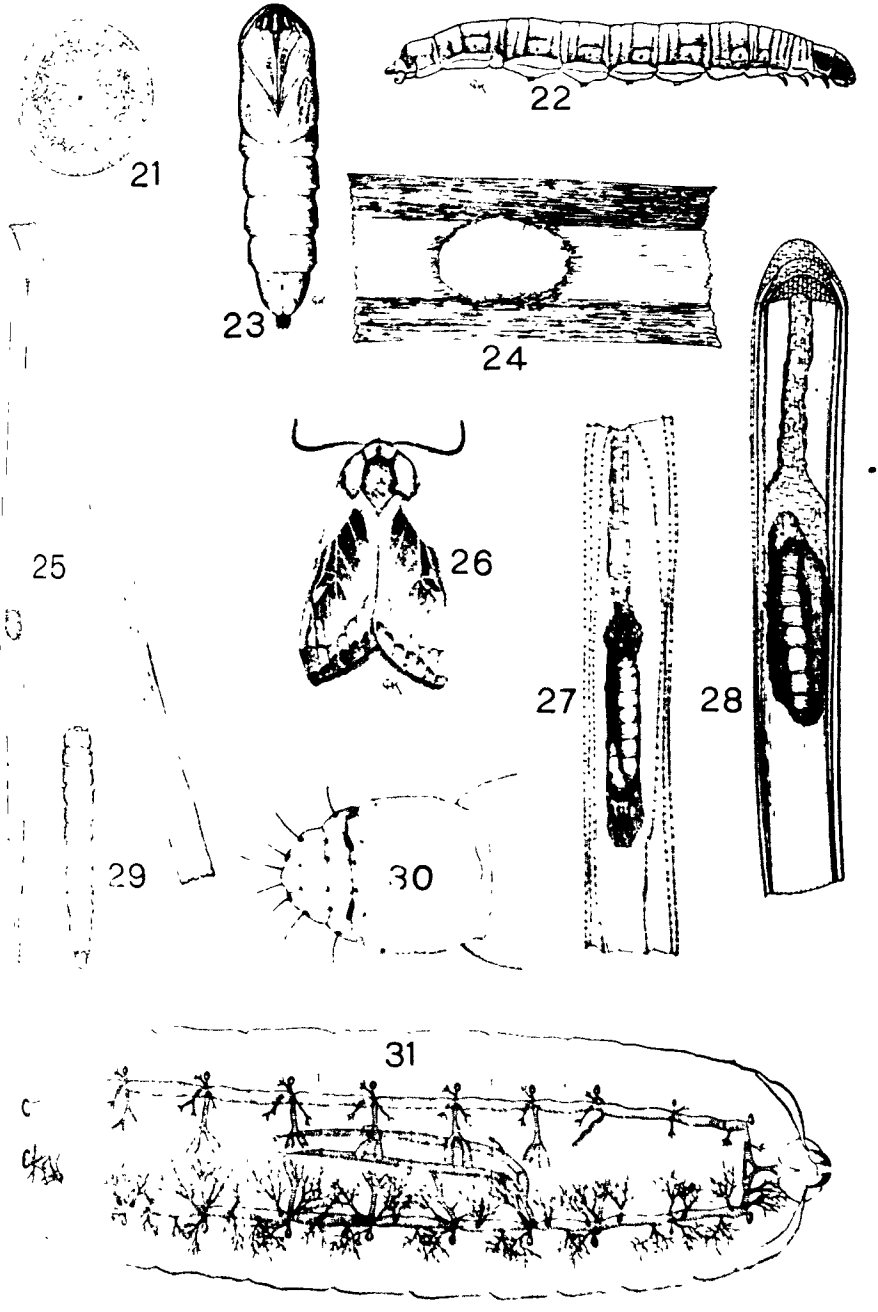
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PLATE XLII

LYMNAECIA PHRAGMITELLA AND NONAGRIA OBLONGA

Lymnaecia phragmitella: 32, Full-grown larva. 34, Pupa. 35, Stalk of cat-tail with leaf turned aside to show where larvae have tunneled in, preparatory to pupation.

Nonagria oblonga: 33, Pupa. 36, Cat-tail plant showing work of larvae. The first-stage larvae have cut the leaf. A mine appears also in the outer sheath. 37, Cat-tail leaf showing early larval work. (The arrow points to the cast skin of the first molt in the transverse mine.)

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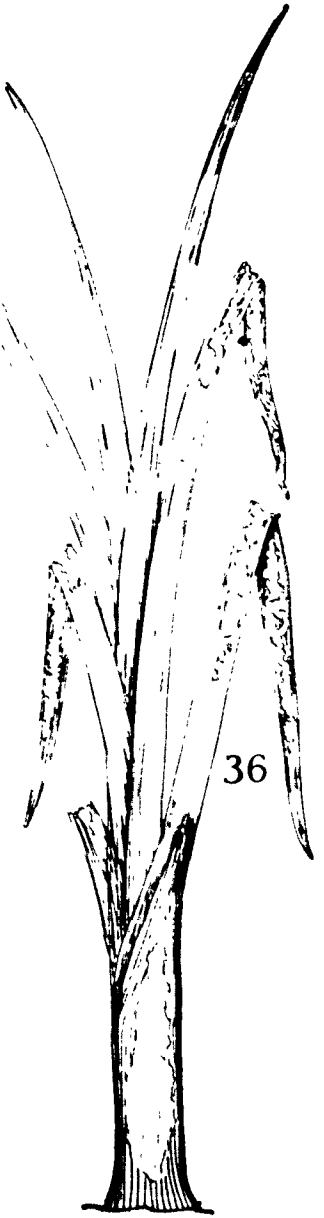

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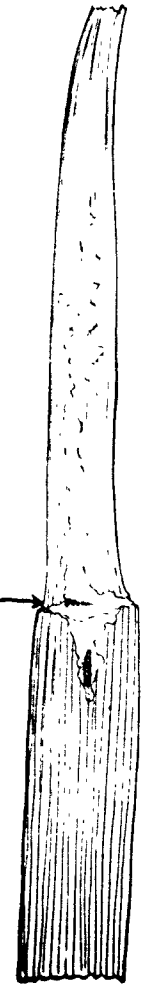

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PLATE XLIII

DIOXYCOLOMIA JULIANALIS

38, Egg. 39, Reticulations on surface of egg. 40, Newly hatched larva. 41, Full-grown **larva.** 42, Axis of cat-tail head cut open to show larval work. 43, Axis of cat-tail head, **showing** opening of larval tunnels. 44, Pupa. 45, Cross section of head of cat-tail, showing **location** of eggs indicated by *a.* 46, Empty egg shell after emergence of larva.

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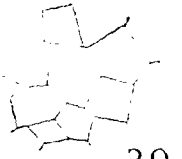

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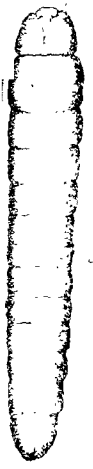

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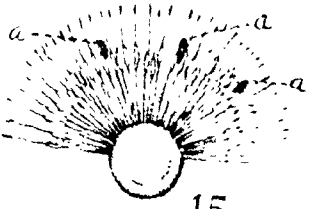

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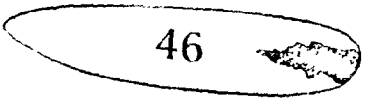

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PLATE XLIV

ISCHNORRHYNCHUS RESEDAE

47, Egg. 48, First-stage nymph. 49, Fourth-stage nymph. 50, Third-stage nymph. 51, Second-stage nymph. 52, Adult female. 53, Enlarged drawing of beak with setae inserted in seed of cat-tail. 54, First-stage nymph. 55, Fifth-stage nymph feeding on seed of cat-tail

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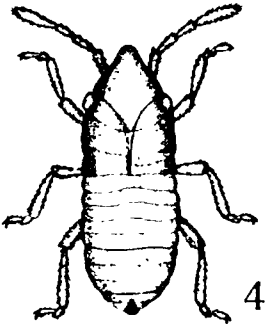

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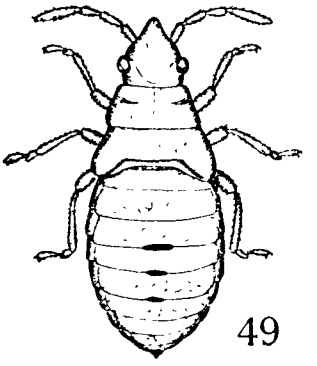

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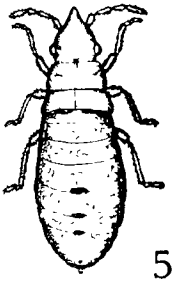

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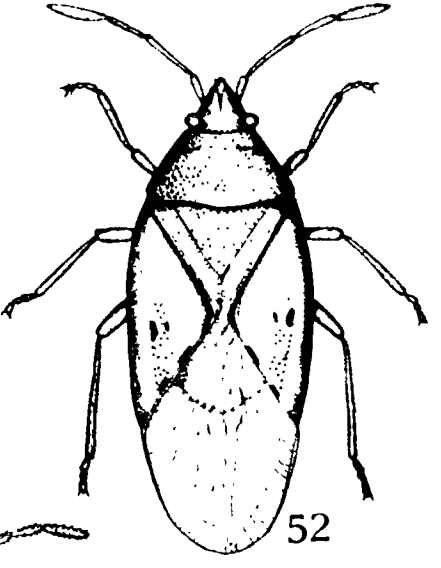

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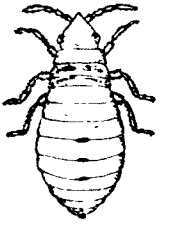

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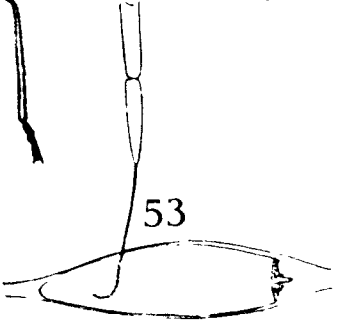

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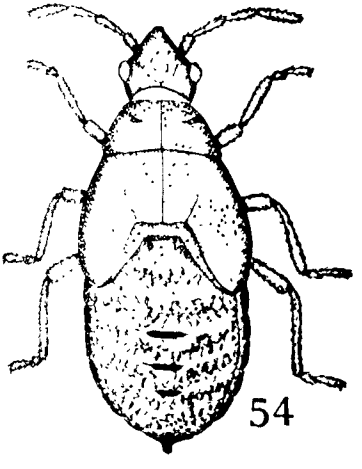

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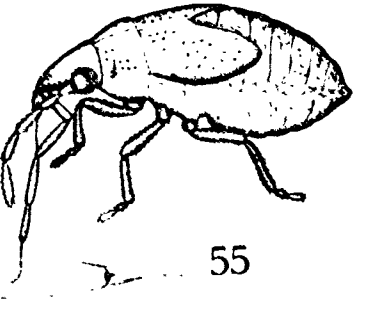

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PLATE XLV

TYPHA LATIFOLIA

56, Two plants connected by underground rhizome, showing also new offsets at bases of old plants. 57, Two pieces of rhizome with outer covering removed to show the relative size of the central starchy core. 58, Leaf with part of the upper epidermis removed to show the structure. 59, Cat-tail heads as they appear in late fall. (The one on the left is infested with the larvae of *Lymnaecia phragmitella*, the one on the right is uninfested.) 60, Cross section of a rhizome

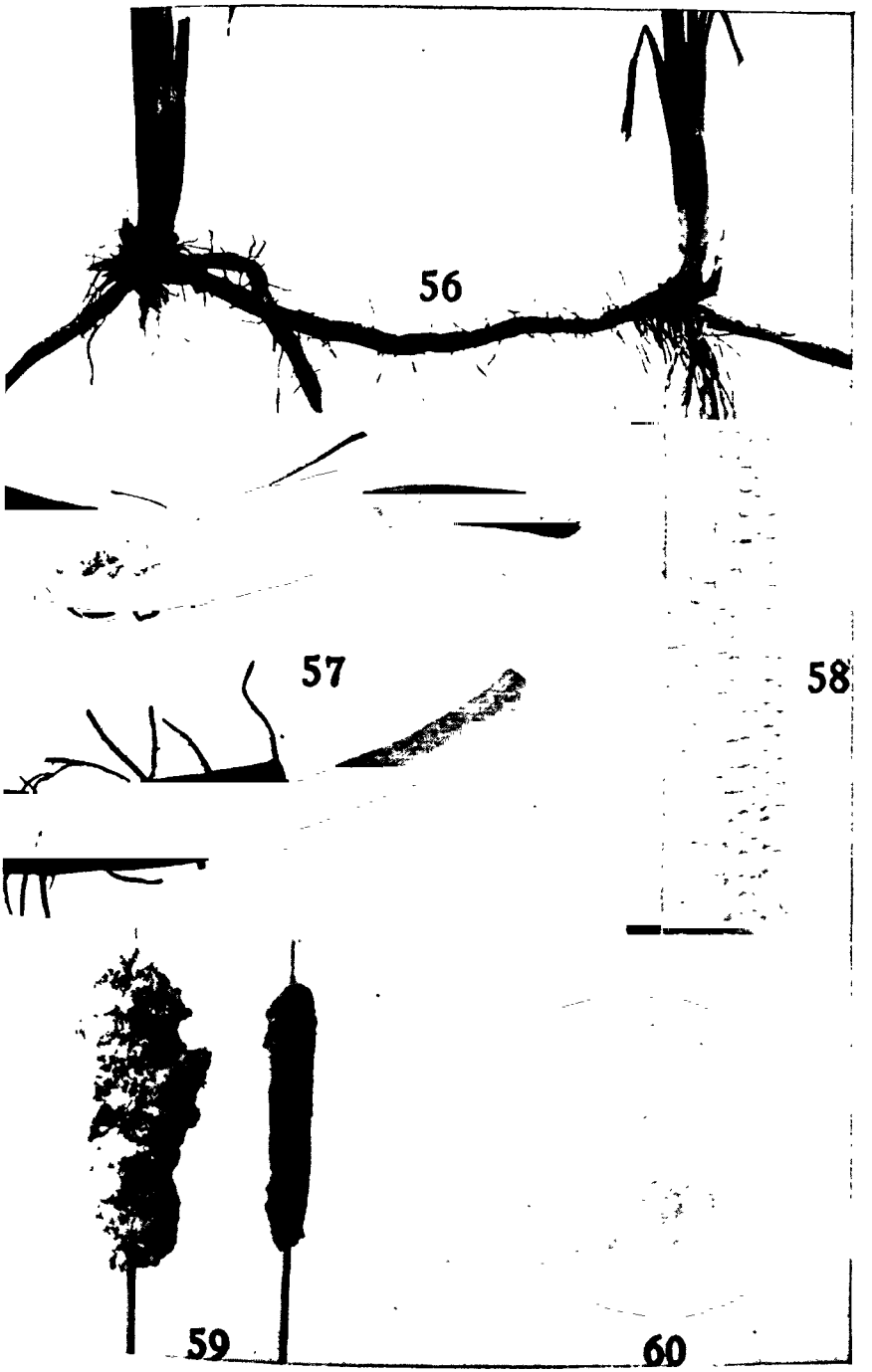
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PLATE XLVI

ARSILONCHE ALBOVENOSA AND ARZAMA OBLIQUA

Arsilonche albovenosa 61, Eggs. 62, Larva feeding on cat-tail leaf. 63, Pupa. 64, Adult
Arzama obliqua: 65, Egg mass. 66, Full-grown larva

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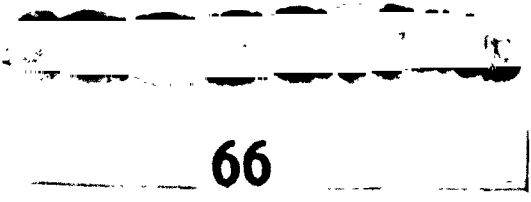

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PLATE XLVII

NONAGRIA OBLONGA AND ARCHIPS OBSOLETANA

Nonagria oblonga: 67, Full-grown larva. 68, Adult. 70, Larva in tunnel in stalk of cat-tail. 71, Pupa

Archips obsoletana: 69, Young cat-tail head showing larval work. (The covering is pulled aside, revealing the head of the larva underneath.) 72, Young cat-tail head showing larval work. (The stigmas of the pistillate flowers are tied together to form a covering for the larva.) 73, Appearance of cat-tail head after wind has torn off covering made by larvae. 74, Pupa. 75, Adult. 76, Larva

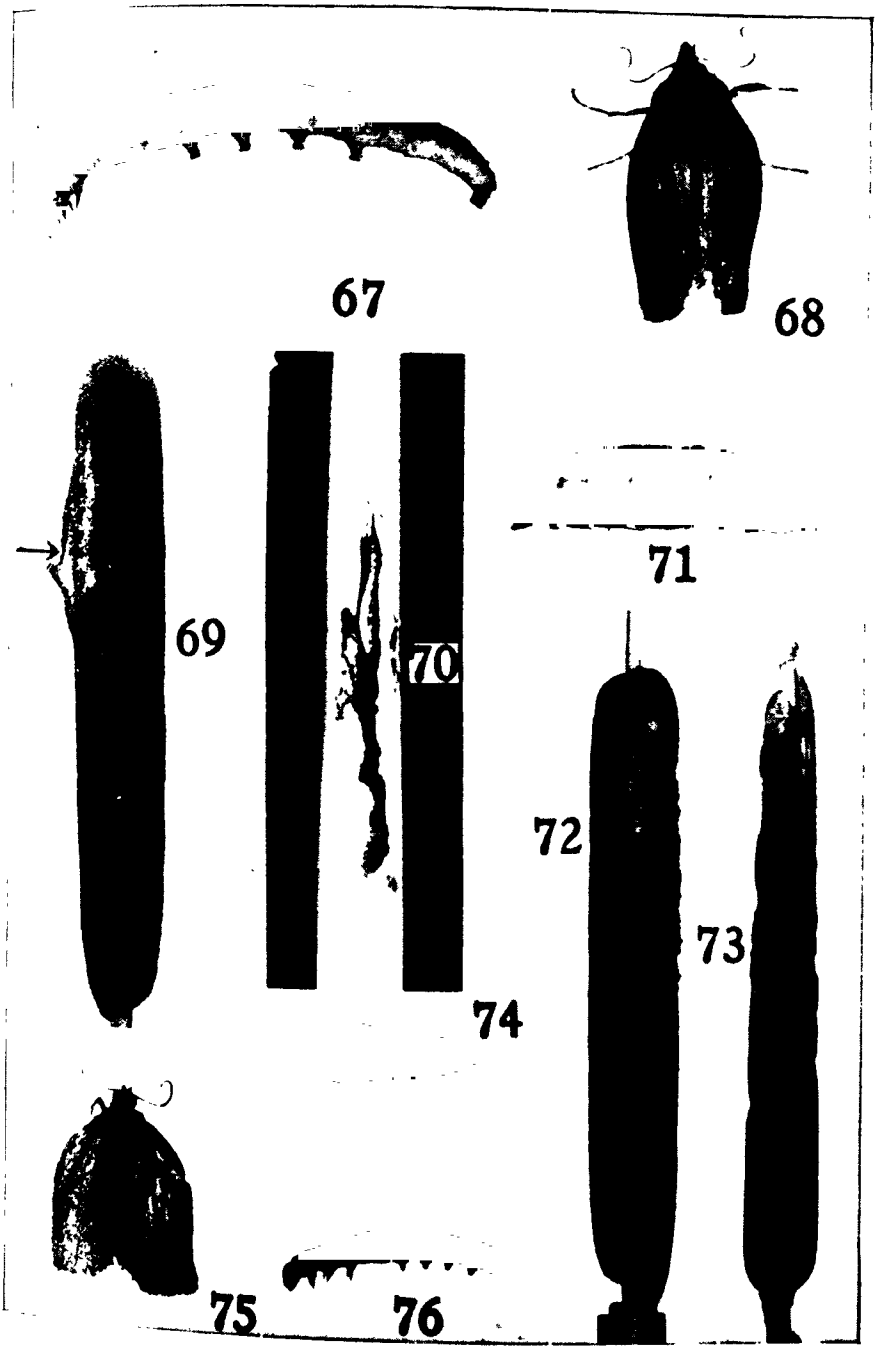
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PLATE XLVIII

CALENDRA PERTINAX, DICYMOLOMIA JULIANALIS, LYMNAECIA PHRAGMITELLA, AND NOTARIS PUNCTICOLLIS

Calendra pertinax 77, Larvae. 78, Adult. 79, Pupa. 80, Pupa in burrow in stalk of cat-tail

Dicymolomia julianalis: 81, Adult

Lymnaecia phragmitella: 82, Cocoons removed from cat-tail head. (One is cut open to show pupa inside)

Notaris punctcollis: 83, Adult

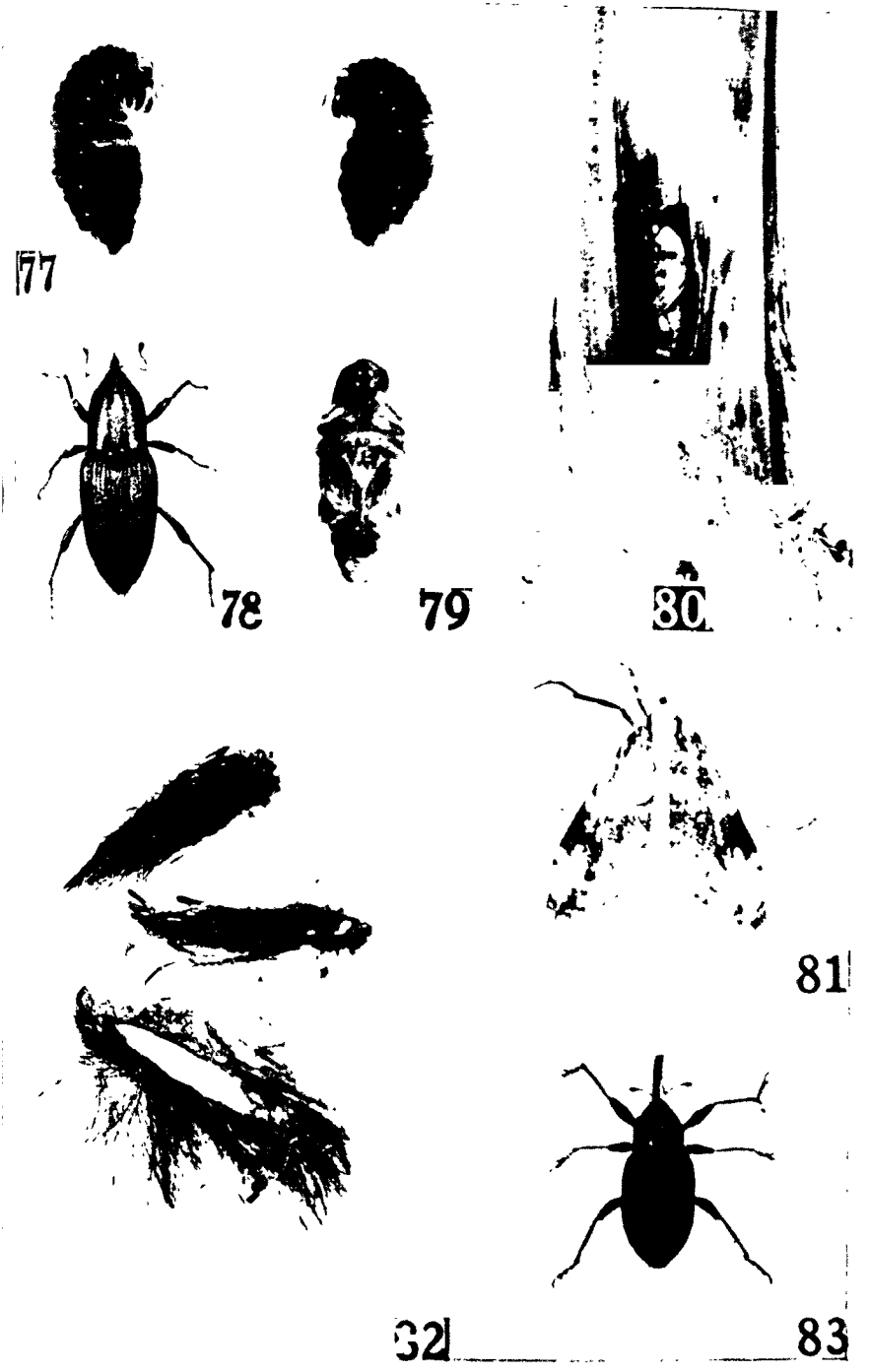
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PLATE XLIX

TYPHA LATIFOLIA

84, A cat-tail patch in July, showing the large number of fluffy heads which are infested with the larvae of *Lymnaecia phragmitella*. 85, Laboratory cat-tail head on which adults of *L. phragmitella* are resting. 86, Nearly mature head of cat-tail, showing evidence of work of young larvae of *L. phragmitella* and *Dicymolomia julianalis*

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NOVEMBER, 1921 MEMOIR 48

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

THE INHERITANCE OF SALMON SILK COLOR IN MAIZE

E. G. ANDERSON

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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THE INHERITANCE OF SALMON SILK COLOR IN MAIZE

THE INHERITANCE OF SALMON SILK COLOR IN MAIZE[1]

E. G. ANDERSON

At the Nebraska State Corn Show of 1908, a number of odd types of corn were gathered together to form a "freak" class. Among them was a "Bronze Pop Corn," so named became of a light bronze color in the pericarp. This ear was obtained by Professor R. A. Emerson, after the exhibit was over, in order to study the inheritance of that pericarp color. The plants grown therefrom were also characterized by brown or brownish silks (Plate LIII). An outcross gave green silks in the F_1. From brown-silked segregates in the progeny of this cross, a true-breeding stock was again obtained. This stock was used in crosses for a study of the inheritance of pericarp color. In one small F_2 of only five plants, there appeared three with green silks and one with brown. The fifth plant had very brilliant salmon or orange-colored silks (Plate LII). This plant was a dilute sun red with red pericarp. It was crossed with red, green, and brown silk colors, and with a purple plant having brown silks. F_1's were grown and selfed to obtain F_2 progenies. The crosses with red and with green silks gave in F_1 red and green silks, respectively. The cross with brown silks gave salmon.

In order to devote more time to studies on aleurone and plant colors and other problems, Dr. Emerson at this point requested the writer to take up the study of these silk colors and their relation to other characters in maize. In his further studies the writer has had the advantage of the hearty cooperation and ever-ready suggestions of Dr. Emerson, and he wishes to acknowledge his sincere gratitude for this help and encouragement.

NOMENCLATURE

The factors referred to in this paper, together with the factor symbols used, are given in the following list:

A a — Anthocyanin pigment. A factor pair for pigmentation of aleurone, sheaths, leaves, anthers, and so forth. (Emerson, 1918, 1921.)

B b — Brown plant color. A factor pair for leaf and sheath pigmentation. (Emerson, 1921.)

[1] Paper No. 83, Department of Plant Breeding, Cornell University, Ithaca, New York.

Pl pl — Purple anthers. A factor pair for pigmentation of anthers sheaths, pericarp, and so forth. (Emerson, 1921.)

These three factor pairs interact to give the following plant color types described by Emerson (1921):

A B Pl — Purple
A B pl — Sun red
A b Pl — Dilute purple
A b pl — Dilute sun red
a B Pl — Brown
a B pl — Green
a b Pl — Green
a b pl — Green

R^r R^g r^r r^g r^{ch} — Red aleurone. A series of allelomorphs affecting anthocyanin pigmentation in aleurone, sheaths, leaves, pericarp, anthers, and silks. (East and Hayes, 1911; Emerson, 1918, 1921.)

P p — Pericarp color. Two of a series of allelomorphs for pericarp coloration. (Emerson, 1911.) The bronze type was so pale in color that it could not be satisfactorily distinguished from white (colorless). Only two symbols are used herein, *P* for red pericarp and *p* for white or bronze pericarp.

Y y — Yellow endosperm. (East and Hayes, 1911; Emerson, 1921.)

Sm sm — Salmon silk color. Described in this paper.

DESCRIPTION OF SILK COLORS

The colors of silk in maize may be described as follows:

1. Green (Plate L). Silks light green, paler below husks; varying from a pure pale green to yellowish green.

2. Red (Plate LI). Silks green, as above, with the addition of a red anthocyanin pigment where exposed to light. The amount of red pigment may vary from a slight trace in the hairs, to sufficient to obscure the green color, giving the silks a deep or dark red color. The darker red silks frequently have some red below the husks. Emerson (1921) has shown this color to be due to the *R* factor. Microscopic sections show anthocyanin pigment in peripheral parts of the silks.[2]

[2] The microscopic sections are prepared as follows: Pigmented tissue is fixed for from twelve to twenty-four hours in a saturated solution of mercuric chloride in 95-per-cent alcohol, and washed with 95-per-cent alcohol without iodine. The usual paraffin method of embedding and sectioning is followed and the preparations are mounted in balsam without staining. Sections from 15 to 25 microns in thickness have proved satisfactory.

GREEN SILKS

[illegible] of the type may be associated with any [illegible] Parts I [illegible] are shown [illegible]

Drawn by Cora M. Preston

RED SILKS

SALMON STICKS

BROWN SER.

3. Salmon (Plate LII). Silks light salmon-orange to salmon. The olor below the husks is similar to that of exposed parts. Microscopic ections show only a faint brownish cast to the tissues thruout the ilks.

4. Brown (Plate LIII). Silks orange-pink to pale salmon or salmon-buff n both exposed and covered parts. Salmon and brown silks intergrade, orming a continuous series. The lighter forms are difficult to distinguish rom the yellowish green silks of No. 1. Both salmon and brown silks ay have red anthocyanin pigment present, as in No. 2.

PRELIMINARY STUDIES AND INDICATIONS

Previous tests had shown salmon silk color to be recessive to green and least partially dominant to brown. Crosses of salmon and brown did t give green color in the F_1. This was taken to indicate that these lors were recessive for a common factor. The anthocyanin pigment esent in red silks was shown to be inherited separately by the occurrence all combination classes (green-red, green, salmon-red, and salmon) the F_2 of red x salmon.

From observation of cultures previously grown, both salmon and brown lks were known to occur on dilute sun red, on sun red, and on purple ants. Their occurrence on brown or green plants had not been recorded. licroscopic examination of the pigments of maize had shown the presence i a purple-red anthocyanin pigment in purple, sun red, dilute purple, nd dilute sun red plants. When the A factor is recessive, no anthocyanin evelops (except traces in the shank and the inner husks of brown plants). nstead, a yellow or brownish pigment may be formed. A similar rela- ion holds with the pericarp pigments. Red pericarp color is due to an range-red or brick-red pigment. Its homolog with recessive A is yellow- h brown, similar in appearance to the brown plant-color pigment. he quantity of pigment in salmon silks is so small that microscopic ections gave little information. But the color of the salmon silks was o similar to the color of thin sections of red pericarp as to suggest the ossible identity of the pigments. The brown silk might, it was thought, e only a dilute form of salmon. These suggestions were further strength- ned by the fact that the original salmon-silked plant had red pericarp nd that the brown silks had been obtained from a plant with bronze

pericarp. Sections of this bronze pericarp showed a small amount of orange pigment.

With these suggestions in mind as a working basis, experiments were planned to test them.

ANALYSIS OF INHERITANCE

Interrelations of green, salmon, and brown silks

The indications just mentioned, regarding the relationships of these silk colors, were all checked and corroborated by further tests. Crosses of green with salmon gave green in the first generation, segregating green and salmon, or green, salmon, and brown, in the second. The distinction between salmon and brown was not sharp. With the small numbers used in these tests, the numbers approach a simple ratio of 3 greens to 1 salmon or to 1 salmon and brown.

Crosses between green and brown likewise gave green, segregating in the F_2 into green and brown or in some cases into green, salmon, and brown. In either case there was about 75 per cent of greens.

Crosses of salmon with brown gave salmon. The F_2 ranged from salmon to brown, with salmon predominating.

These results show that there is a common factor pair which differentiates between green on the one hand and salmon and brown on the other. This pair is herein referred to as the salmon-silk factor pair and is designated by the symbols *Sm sm*.

The difference between salmon and brown silks is not explained by these simple tests, tho the occurrence of brown silks in the progenies of outcrosses of salmon, and vice versa, is at least a strong indication of one or more modifying factors.

Relation of salmon silks to pericarp color

In order to test the relationship of the salmon factor to the factor for pericarp color, two series of crosses were made. In the first, a colored-pericarp, green-silked plant (*P Sm*) was crossed with a light-bronze-pericarp, brown-silked plant (*p sm*). In the second, two white-pericarp green-silked plants (*p Sm*) were crossed with the original salmon-silked plant, which had red pericarp (*P sm*). The F_1's were crossed with the double recessive. The results are given in table 1:

TABLE 1. RELATION OF SALMON SILKS TO PERICARP COLOR

I. Backcrosses of *P Sm* x *p sm* with *p sm*

Pedigree no.	*P Sm*	*P sm*	*p Sm*	*p sm*	Total
253–4	9	6	11	29	
255	5	11	12	10	
256	9	6	15	7	
777–8	41	32	41	39	
Totals	64	55	79	76	274

Observed per cent of recombinations 48.9
Per cent expected with independent segregation . . . . 50.0±2.0

II. Backcrosses of *p Sm* x *P sm* with *p sm*

Pedigree no.	*P Sm*	*P sm*	*p Sm*	*p sm*	Total
238–9	43	61	51	53	
241–2	31	28	31	38	
779–80	23	25	25	28	
781–2	43	40	50	40	
Totals	140	154	157	159	610

Observed per cent of recombinations 48.9
Per cent expected with independent segregation . . . . . 50.0±1.1

The observed per cent of recombinations is 48.9 in both series, which is in very close agreement with the expectancy for independent segregation of *P* and *Sm*.

In order to determine the possible relation of pericarp color to the difference between salmon and brown silks, a light-pericarp, brown-silked plant was crossed with a red-pericarp salmon. This was backcrossed

with a light-pericarp, brown-silked plant similar to the one parent. The silk colors were noted during the summer. It was impossible to make any sharp separations, for the colors varied from a deep salmon to a typical or even light brown. The presence of red anthocyanin pigment added to the difficulty, as did also the fact that the silks could not be noted at the same stage. So they were only roughly classified, the classifications from time to time not being entirely comparable. The notes were underscored for a number of good salmons and browns. The pericarp colors were determined in the fall. The results are given in table 2.

TABLE 2. BACKCROSSES OF *p, sm* x *P sm* WITH *p sm*

Silk color	Red pericarp	White or light bronze
Salmon, underscored	17	0
Salmon	167	19
Salmon —	25	10
Salmon-brown	33	11
Brown-salmon	10	24
Brown +	24	65
Brown	11	172
Brown, underscored	0	14

It will be seen from this table that most of the red-pericarp plants had been noted as having salmon silks, while the light-pericarp ones were mostly noted as having brown silks. It is also significant that, of those cases in which salmon was underscored, all had red pericarp. Likewise, of the cases in which brown was underscored, all had light pericarp. Since the salmon factor pair *Sm sm* has been shown to segregate independently of the factor pair *P p* for pericarp color, this variation cannot be due to the *Sm sm* pair. The conclusion is drawn that the intensity of pigmentation of silks recessive for *sm* is largely a function of the intensity of pigmentation of the pericarp or of some factor closely associated with the factor for pericarp color. The former view is substantiated

by the fact that no selfed progenies from light-pericarp plants have ever given any good salmon silks, while progenies from red-pericarp plants have always given some salmon silks even tho the parents had been noted otherwise. No brown silks have been found in families breeding true for red pericarp.

Relation of salmon silks to the B and Pl factors for plant color

Several crosses made with salmon silks involved the *B* factor. Both F_1 combinations, *B Sm* x *b sm* and *B sm* x *b Sm*, were backcrossed with the double recessive. The results (table 3) show independent segregation of these factors.

TABLE 3. RELATION OF SALMON SILKS TO THE *B* AND *Pl* FACTORS FOR PLANT COLOR

I. Backcrosses of *B Sm* x *b sm* with *b sm*•

Pedigree no.	*B Sm*	*B sm*	*b Sm*	*b sm*	Total
241–2	25	24	39	41	
779–80	21	19	28	35	
Totals	46	43	67	76	232

Observed per cent of recombinations 47.4
Per cent expected with independent segregation . . . . . 50.0±2.2

II. Backcrosses of *B sm* x *b Sm* with *b sm*

Pedigree no.	*B Sm*	*B sm*	*b Sm*	*b sm*	Total
774 6	78	62	80	53	273

Observed per cent of recombinations 47.6
Per cent expected with independent segregation . . . . . 50.0±2.0

One of the crosses of the original salmon-silked plant, *A b pl sm*, was with a purple plant with green silks, *A B Pl Sm*, related to the bronze stock. The progeny consisted of purple and sun red plants with green and salmon silks, showing the parent to have been heterozygous for both *Pl* and *Sm*. Two small plantings gave the following distributions *Pl Sm*, 26; *Pl sm*, 7; *pl Sm*, 4; *pl sm*, 23; whereas equality of the four classes would be expected if the factors were independent. This was obviously a linkage relation. The factor *Pl* was known to be linked with a factor *Y* for yellow endosperm (Emerson, 1921). Tests of the linkage relations within this group are given in a later section of this paper.

Relation of salmon silks to the A factor

From an outcross of the original salmon-silked plant with one heterozygous for brown silks and for the *A* factor, several plants were selfed. One sun red plant was homozygous recessive for the salmon silk factor and heterozygous for *A* and *B*. Thirty-four sun red and dilute sun red plants had salmon or brown silks. Two others were first noted as green but were presumably a light brown, both having white pericarp. Eleven green plants appeared, all having green silks. Later observations on green and brown plants of other families segregating for both *a* and *sm* have likewise failed to reveal any green plants with other than green silks. That this is not due to linkage is shown by the linkage of *Sm* with the *Pl* factor, which is known to be independent of *A*, and by the fact that the green plants have green silks in families that are homozygous recessive *sm*.

Relation of salmon silks to the R factor

Two questions of interest arose regarding the relation of salmon silk color to the *R* series of allelomorphs. The first was the relation of cherry pericarp color to the intensity of color in salmon or brown silks, the second was the possibility of the occurrence of salmon silks on green plants of the constitution R^g *A b Pl* or R^g *A b pl*.

To test the effect of cherry pericarp, a sun red with brown silks, *A B pl sm* r^r, was crossed with a dilute purple with cherry pericarp and green silks, *A b Pl Sm* r^{ch}. Backcrosses gave a few plants with cherry pericarp and brown silks. They were not noticeably different in silk color from the white-pericarp plants of the same families.

To test for the occurrence of salmon silks on green plants of the constitution *R^g A b Pl* or *R^g A b pl*, a dilute purple plant with salmon silks was crossed with a green plant of the constitution *R^g A b pl*. Two of the F_1 plants were selfed. Purple seeds only were planted. These gave 44 dilute purples and dilute sun reds, of which 32 had green silks and 12 had salmon. There were 25 green plants, *R^g A b*, 18 of which had green silks; the other 7 had typical salmon and brown silks.

From these two tests, it may be concluded that salmon silk color is not dependent on the *R* factor nor is it noticeably influenced thereby. This is similar to the relation between red pericarp color and *R^g* (Emerson, 1921).

Summary of inheritance

Salmon and brown silks are recessive to green silks by a single factor pair, *Sm sm*.

This factor, *Sm*, is independent in inheritance from *P* (pericarp), *A* (aleurone and plant color), *B* (plant color), and *R* (aleurone, plant color, cherry pericarp, and red silk color).

It is linked with the factor *Pl* (plant color), and consequently also with *Y* (yellow endosperm).

Dominant *A* is necessary for the production of salmon or brown silk color; that is, the combination *a a sm sm* is green.

The intensity of pigmentation of salmon-brown silks is directly related to the intensity of pigmentation of the pericarp.

The relation of the factors *A*, *Sm*, and *P* to silk color may be represented schematically as follows:

A Sm P = Green	*a Sm P* = Green
A Sm p = Green	*a Sm p* = Green
A sm P = Salmon	*a sm P* = Green
A sm p = Brown	*a sm p* = Green

LINKAGE RELATIONS OF *Y*, *Pl*, AND *Sm*

Preliminary tests of linkage of Pl and Sm

The first indication of the linkage of the *Sm* and *Pl* factors was observed in the progeny of an outcross of the original salmon with a purple plant having green silks. This plant proved to be heterozygous for both *Sm*

and *Pl*. To the distribution given on page 546 may be added the data from a duplicate planting by Dr. Emerson:

	Pl Sm	*Pl sm*	*pl Sm*	*pl sm*	Per cent of crossing-over
111–2	26	7	4	23	
From Emerson	25	9	4	38	
	51	16	8	61	17.6

Two other backcrosses were then made, which the following year gave the results:

	Pl Sm	*Pl sm*	*pl Sm*	*pl sm*	Per cent of crossing-over
238–9	76	24	20	93	20.3
241	60	4	4	66	6.3

Construction and results of three-point tests

In the meantime, crosses were made to involve the *Y* factor for yellow endosperm in addition to *Pl* and *Sm*, since *Y* and *Pl* were known to be linked. To get a satisfactory three-point backcross test involved several difficulties, as follows:

1. Yellow endosperm is not easily distinguished from white if brought in only by the pollen. This is assumed to be due to the dominant *Y*'s being represented only once in the triple-fusion endosperm nucleus. It is therefore desirable that the F_1 plants should be used as female parents in the backcrosses.

2. Brown silks are not readily separated from green. This difficulty can be avoided only by having red pericarp in each plant. But the presence of red pericarp obscures the color of the endosperm. So in order to make endosperm separations possible, the female parent of the backcross must be free from red pericarp.

3. Purple and dilute purple plants usually have some purplish pigment in the pericarp, which in some cases interferes with the classification of yellow endosperm.

4. The dominant *A* factor must be present in every individual where silk color separations are to be made.

5. Aleurone color must be avoided.

6. Presence of the dominant *B* factor, while not affecting accuracy, would nevertheless facilitate note-taking by making all the plants of two sharply differentiated classes, purple and sun red.

To avoid as many as possible of these difficulties and accomplish the results within the shortest period of years, the following procedure was put into effect: Crosses were made involving the factors *Y*, *Pl*, and *Sm* in different combinations. In all of these crosses, pericarp color and also the *R* factor for aleurone color were kept recessive. At the same time, an attempt was made to find or isolate a stock of the triple recessive of the desired composition. Tests of all available salmon-silk material revealed two closely related families breeding true for red pericarp, white endosperm, nd recessive *r*. Both families consisted of sun red and dilute sun red lants showing the *B* factor to have been heterozygous. These were used he following year in the backcrosses. Their composition was *y y pl pl sm sm r r P P A A*, some plants being homozygous and some heterozygous or dominant *B*. Pollen of these plants was used on silks of the F_1 rosses.

These backcrosses were made in 1918 and the progenies were grown in 1919. The results are given in table 4 (page 550). The percentages of crossing-over are: *Y-Pl*, 28.9; *Pl-Sm*, 9.1; *Y-Sm*, 36.6, showing their relative order to be *Y-Pl-Sm*.

While material for these tests was being built up, some much less satisfactory backcrosses were made by pollinating white-endosperm, brown-silked, dilute sun red plants with pollen from crosses involving *Y*, *Pl*, and *Sm*. These were grown in 1918. The results are given in table 5 (page 551).

A summary of the percentages of crossing-over is given in table 6 (page 552).

The chromosome map

From the totals of all the data obtained on these linkage relations, the observed percentages of crossing-over are found to be 29.70 for *Y-Pl*, 10.01 for *Pl-Sm*, and 36.79 for *Y-Sm*. This shows their relative map order to be *Y-Pl-Sm*. The distance from *Y* to *Pl* as observed is 29.7,

TABLE 4. BACKCROSSES INVOLVING *Y, Pl,* AND *Sm*, 1919

Pedigree no.	Character of F_1	Non-crossovers		Crossovers *y-pl*		Crossovers *pl-sm*		Double crossovers	
		Y Pl Sm	*y pl sm*	*Y pl sm*	*y Pl Sm*	*Y Pl sm*	*y pl Sm*	*Y pl Sm*	*y Pl sm*
1451–3	*y pl sm* x *Y Pl Sm*	79	74	57	48	7	19	0	3
1454–6	*y pl sm* x *Y Pl Sm*	32	24	20	16	1	4	0	1
		Y pl Sm	*y Pl sm*	*Y Pl sm*	*y pl Sm*	*Y pl sm*	*y Pl Sm*	*Y Pl Sm*	*y pl sm*
1457–9	*Y pl Sm* x *y Pl sm*	160	145	75	79	13	24	0	0
1460–2	*Y pl Sm* x *y Pl sm*	144	113	49	71	14	18	3	1
1463–6	*Y pl Sm* x *y Pl sm*	132	119	41	56	18	8	2	0
		Y Pl sm	*y pl Sm*	*Y pl Sm*	*y Pl sm*	*Y Pl Sm*	*y pl sm*	*Y pl sm*	*y Pl Sm*
1467–8	*y pl Sm* x *Y Pl sm*	72	67	16	20	2	10	0	0
1469–70	*y pl Sm* x *Y Pl sm*	124	99	39	36	10	10	0	0
1471–3	*y pl Sm* x *Y Pl sm*	109	99	52	68	16	10	0	1
		Y pl sm	*y Pl Sm*	*Y Pl Sm*	*y pl sm*	*Y pl Sm*	*y Pl sm*	*Y Pl sm*	*y pl Sm*
1476–7	*Y pl sm* x *y Pl Sm*	43	45	23	13	13	5	1	0
1478–80	*Y pl sm* x *y Pl Sm*	69	83	25	26	11	21	1	0
1481–2	*Y pl sm* x *y Pl Sm*	58	50	18	24	15	11	4	4
Totals		1,940		872		260		21	

TABLE 5. BACKCROSSES INVOLVING *Y*, *Pl*, AND *Sm*, 1918

Pedigree no.	Character of F_1	Non-crossovers		Crossovers *Y-Pl*		Crossovers *Pl-Sm*		Double crossovers	
		Y pl sm	*y Pl Sm*	*Y Pl Sm*	*y pl sm*	*Y pl Sm*	*y Pl sm*	*Y Pl sm*	*y pl Sm*
772–3	*Y pl sm* x *y Pl Sm*	51	73	43	29	9	7	2	5
774–6	*Y pl sm* x *y Pl Sm*	63	94	50	40	13	8	4	1
781–2	*Y pl sm* x *y Pl Sm*	49	66	24	20	5	7	4	2
		Y Pl Sm	*y pl sm*	*Y pl sm*	*y Pl Sm*	*Y Pl sm*	*y pl Sm*	*Y pl Sm*	*y Pl sm*
777–8	*y pl sm* x *Y Pl Sm*	51	51	14	28	9	4	1	0
779–80	*Y Pl Sm* x *y pl sm*	29	31	18	12	4	4	4	1
Totals		358		278		70		24	

TABLE 6. SUMMARY OF LINKAGE DATA

Pedigree no.	Total number of plants	Percentage of crossing-over		
		Y-Pl	*Pl-Sm*	*Y-Sm*
111–2	136		17 5	
238–9	213		20 7	
241	134	..	6 0	
Totals	483		15 73	
772–3	219	36 1	10 5	40 2
774–6	273	34 8	9 5	40 7
781–2	177	28 2	10 2	31 6
777–8	158	27 2	8 9	34 8
779–80	103	34 0	12 6	36 9
Totals 1918	930	32 47	10 11	37 42
1451–3	287	37 7	10 1	45 6
1454–6	98	37 8	6 1	41 8
1457–9	496	31 0	7 5	38 5
1460–2	413	30 0	8 7	36 8
1463 6	376	26 3	7 4	32 7
1467–8	187	19 3	6 4	25 7
1469–70	318	23 6	6 3	29 9
1471–3	355	34 1	7 6	41 1
1476–7	143	25 9	13 3	37 8
1478–80	236	22 0	14 0	35 2
1481–2	184	27 2	18 5	37 0
Totals 1919	3,093	28 87	9 09	36 60
Totals 1918–1919	4,023	29 70	9 32	36 79
Totals of all data	4,506	..	10 01	..

or approximately 30 units. Since in such long distances double crossing-over may be expected, a corrected map distance should be 30 plus twice the per cent of unobserved double crossovers between the two points. But with the high amount of interference indicated by the small number of observed coincident crossovers in the two regions *Y-Pl* and *Pl-Sm*, the corrected value for these data is probably not much above 30 or 35. The value 30 for the map distance between *Pl* and *Sm* is probably correct for these data.

It should be understood that the chromosome map is primarily a graphic representation of the data on linkage relationships. Its correspondence with actual positions on the chromosome itself is not implied, tho the work of Morgan and his coworkers has given much evidence of at least a correspondence between relative map order and the actual relative position of the genes in the chromosome.

The variability of the percentages of crossing-over shown in table 6 is not greater than would be expected of heterogeneous data. Gowen (1919) has shown crossing-over in Drosophila to be an extremely variable phenomenon. Plough (1917) has shown it to be modified by temperature, and Bridges (1915) by age of the individual. The subject of variation of crossing-over in maize must remain for study with less difficult characters than those involved in these experiments.

The distributions when the F_1's were used as pistillate and as staminate parents give nearly the same averages, but the data are inadequate for any conclusion except that the crossing-over is not widely different in the two cases.

Coincidence of crossing-over

Coincidence of crossing-over in two regions of a chromosome is the ratio of observed coincident (simultaneous) crossing-over to the calculated expectancy. The expectancy is the product of the percentages of crossing-over of the two regions. The actual calculation may be simplified, as shown by Weinstein (1918). The derived formula is

$$\text{Coincidence} = \frac{xn}{ab}$$

in which n = the total number of individuals,

x = the number of coincident crossovers,

a and b = the total number of crossovers in the respective regions.

The coincidence of crossing-over in the two regions *Y-Pl* and *Pl-Sm*, calculated from tables 4 and 5, is as follows:

From table 4:

$$\text{Coincidence} = \frac{21 \times 3093}{893 \times 281} = 0.26$$

From table 5:

$$\text{Coincidence} = \frac{24 \times 930}{302 \times 94} = 0.79$$

From combined data of tables 4 and 5:

$$\text{Coincidence} = \frac{45 \times 4023}{1195 \times 375} = 0.40$$

These values are entirely comparable with those listed by Weinstein (1918) for Drosophila. From this and the similarity of all phases of linkage and crossing-over, it is evident that the mechanism of crossing-over in maize is not strikingly different from that in Drosophila except in one respect. In Drosophila, crossing-over occurs in oogenesis only, in spermatogenesis not at all. In maize the phenomena of crossing-over are at least of the same order in both megasporogenesis and microsporogenesis.

Summary of linkage studies

The factor *Sm* for salmon silk color is shown to be linked with the factor *Y* for yellow endosperm and the factor *Pl* for plant and anther color.

The relative order of these three factors is *Y-Pl-Sm*.

The amount of crossing-over between *Y* and *Pl* is about 30 per cent; between *Pl* and *Sm* it is about 10 per cent.

The observed coincidence of crossing-over in the two regions *Y-Pl* and *Pl-Sm* was about 0.4

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Memoir 41, *Lysimeter Experiments—II*, the seventh preceding number in this series of publications, was mailed on November 16, 1921.

NOVEMBER, 1921 MEMOIR 49

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

THE BIOLOGY OF EPHYDRA SUBOPACA LOEW.

CHIH PING

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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THE BIOLOGY OF EPHYDRA SUBOPACA LOEW

THE BIOLOGY OF EPHYDRA SUBOPACA LOEW

CHIH PING

The observations and experiments herein described were begun in the summer of 1916 and covered a period of two years. The main purpose of the study was to investigate the habits, activities, and relations to environment of *Ephydra subopaca* throughout all the stages in its life history, and to solve the problem of its unique habits and adaptations. During the period, daily field data were taken at the salt pools beside the east bank of Cayuga Lake, and various other salt-water areas in the vicinity of Ithaca, New York, were occasionally visited.

HISTORY OF THE SPECIES

The adult of this species was first described by Loew (1864) from Connecticut. Following this, Packard (1868) described both the puparium and the adult as *Ephydra halophila* (a preoccupied name), from brine pools in Illinois. The occurrence of this species at Charlotte Harbor, Florida, was recorded by Johnson (1895), and at several localities in New Jersey by Smith (1890). Johnson (1904) also records this species at Atlantic City and Seaside Park, New Jersey. All the works mentioned above are mere descriptions or records of occurrence, but none has anything bearing on habits, development, or life history. The most recent and detailed work on the biology of *Ephydra subopaca* is by Aldrich, in whose article on some western species (1912a) are discussed the habits, food, and some interesting features of both the adult and the immature stages. However, the egg was not described, oviposition and mating had not been observed, and the life history was hitherto incomplete. Neither had ecological phenomena been investigated in detail.

DISTRIBUTION AND RANGE IN ITHACA AND VICINITY

Only two species of Ephydra, as far as records show, are found in New York State. The species *Ephydra subopaca* is found in Ithaca and in

AUTHOR'S ACKNOWLEDGMENTS. The author wishes to acknowledge his indebtedness to Professors E. M. Chamot, J. R. Schramm, W. A. Riley, and H. O. Buckman, Doctors L. A. Hausman, C. P. Alexander, and F. R. Georgia, and Messrs C. R. Yih and K. Y. Wong, for assistance in their respective fields, and to Professors J. G. Needham and O. A. Johannsen for advice and guidance during the progress of the work.

neighboring localities wherever salt pools occur. The larvae and pupae live in water of various densities and in a variety of other physical conditions, but a certain percentage of salt must be present in the water. The species can live in fresh water only for a very brief period. The species was found living at two places in Ithaca, the first being an old salt plant, near the Inlet, where there were two permanent pools, in which the water was brownish in color and salty in taste. All stages of the species were collected here in the summer of 1916, but unfortunately, in the year following, one pool was filled with dirt, while the other one became entirely fresh, and no more of this species could be found there.

The second place where this species was and can yet be found, is at the east bank of Cayuga Lake, at the Remington Salt Works, where the salt wells are the sources of the overflow of brine water from an intensive area. At this place the water is strong in salt, and the pools, ditches, and overflowed areas abound in *Ephydra subopaca* in all stages of development. Throughout the two summers and a part of the winter of 1916-17, most of the field observations were made at this latter place and practically all the ecological phenomena discussed herein are related to this locality.

At Ludlowville, on the east shore of Cayuga Lake, a fairly wide area is flooded at certain seasons by the brine water from salt wells. This condition is by no means permanent, and the salt water is frequently dried up in midsummer. However, in the summer of 1917 this place was visited at intervals for making observations and for collecting. Next to the permanent pools at Ithaca, the best place, where enormous numbers of this species are found and where the permanent pools, ditches, and wide, overflowed areas afford excellent opportunities for field work, is at Solvay, Syracuse.

Owing to convenience of location, most of the ecological observations were made at the salt pools at Ithaca. There are eight pools, six of which are located in series, about one and a half meters apart, situated from north to south along the east side of the lake. The six pools are designated as A, B, C, D, E, and F. The other two, I and H, are situated further away from the lake shore, toward the east, and along the roadside. In addition to the eight pools, overflowed areas, large and small, are scattered here and there between the pools, covering an estimated area of forty square meters.

PHYSICAL FEATURES OF SALT POOLS

Soil

Although these pools are scarcely over a year old, due to the destruction nd reconstruction of the salt works within two years, the physical features n them are perfectly natural. Pools A to F are located close to one side f a delta deposit of Hamilton shales on the east shore of Cayuga Lake. he soil at the east side of the pools is largely made up of such deposit nd is elevated about one meter higher than the soil at the other side, hich is on the ground level. The soil of the higher side has shales mixed ith clay, while that of the lower side, which composes three-fourths of he circumference and slopes down to the bottom, is entirely free from hales and is a homogeneous, purely clay soil.

The condition in pools I and II, and in the overflowed areas, is entirely lfferent. The overflowed areas are composed of sandy loam with some rganic materials, such as grass stems, and with small fragments of boards nd animal excrement sparingly scattered over.

Pools I and II, in which the water is much deeper, possess some different eatures as far as soil is concerned. They are situated quite away from he delta deposit, and no shales have been found in them. One side of hese two pools is adjacent to a path built up with a mixture of cinders nd sandy loam and their bottoms are on the same ground level with the verflowed areas. Glancing into the pools through the transparent and omparatively fresh brine water, the homogeneous grayish black color of the oil affirms that the entire bottom and the slopes below the water sur- ace consist of nothing but sandy loam mixed with coarse cinders.

Water

The pools, in contrast to the overflowed areas, are permanent. The eneral condition of the water varies according to rainfall, sunshine, alinity, and biological content, and sometimes to artificial causes also. The verage diameter of these pools measures from 1.35 to 1.4 meters, and he depth from 0.35 to 0.4 meter; that of the overflowed areas, from 5 to 6 entimeters. The color of the water in pools A to F is generally brownish. When rainfalls are frequent, the brownish color fades away, changing to lightly grayish green about 3 or 4 centimeters below the surface. The ater in the overflowed areas remains fairly clear owing to its shallowness

and temporary existence. Generally a thick layer of dark brown scum prevails here and there over the surface, but the clearness of the water underneath is not affected. Pools I and II were dug in the latter part of the summer of 1917; unlike the water in the older pools, the water in these has continued perfectly clear all the time, so the presence or absence of color is due to the difference in age of these pools. Pools A to F, because of their proximity to a much-used rail track, have been polluted to a certain extent by oily substances and animal feces. This is true also of some parts of the overflowed areas. Pools E and F were spoiled in the latter part of the season by being filled in with lumber fragments and a great quantity of waste salt. The general condition of the water in the different pools from August 17, 1917, to October 17, 1917, has been recorded as follows:

Pool	August 17	August 19	August 22	September 7	September 18	October 3	October 17
A	Greenish brown	Pale greenish	Greasy films	Greasy films	Greasy films, grayish	Greasy films, grayish	Greasy films, grayish
B	Green, brownish at surface	Pale greenish	Somewhat clear thin greasy films	Clear, slightly pale greenish	Greasy films, greenish	Greasy films, greenish brown	Greasy films, grayish
C	Brownish, slightly dark	Pale greenish	Thin greasy films	Thick greasy film, brownish	Pale greenish brown	Pale greenish brown	Greasy films, grayish
D	Brownish, slightly dark	Brownish	Thin greasy films	Deep green	Greenish brown	Greenish brown	Brownish
E	Somewhat clear	Brownish	Spoiled				
F		Brownish	Spoiled				

I, II } Clear throughout the season

The water in all these pools, as well as in the overflowed areas, remains stagnant all the time. When rain is in excess, water may flow into them from the near-by ditches or from some areas that are located on a higher level; but throughout the greater part of the season the stagnant condition is seldom disturbed. The quantity of water in these pools is decreased by evaporation during dry weather. The pools themselves, however, did not dry up during the seasons of observation. Being so limited in area and so sheltered in location, the surface of the pools is not likely to be disturbed by the wind.

Although situated close to one another, the density and salinity in the pools have noticeable fluctuations and increase from north toward south in their range; this is perhaps due to their gradual approach to the spot where the loading of salt takes place, which is near Pool F. The following shows the difference:

Pool	Density		Salinity (per cent)	
	August 10*	September 22†	August 16‡	August 16§
A	1 5	4	3 90	1 90
B	2 0	5	1 76	2 28
C	4 0	6	2 68	5 35
D	5 0	6	4 20	6 84
E	7 0		5 58	9 70
F	7 0		7 40	9 70
I		9		
H		11		...

*Determined in the laboratory
†Determined in the field
‡Analyzed after one day in the laboratory.
§Analyzed after being kept for three days in the laboratory.

BIOLOGICAL CONTENTS OF SALT POOLS

As the pools are so limited in size and since none of them have been in existence for more than a year, it is only natural that no large plants have ever been found growing in them. Moreover, the salinity and density of the water account for the total absence of some larger animals that commonly inhabit fresh water pools. The only fauna and flora that are common here are plancton forms, the plants of which serve as food through-

out the season for *Ephydra subopaca* in both the larval and the adult stages when active. The plancton enriching pools A to E gives color to the salt water in very different degrees. Plancton is the only organic material from which the inhabiting fauna obtains its subsistence. In the summer season the changing colors and varying content of the water in these pools mark the increase and decrease in abundance of the microscopic forms of one kind or another. During frequent surveys of pools A to F made in the middle and later part of the summer, it was found that the plant life therein included large numbers of Chlamydomonae, Navicula, and bacteria, and the animals, numerous Actinophrys and Monas, a few Astasia and amoebas, and a very few Halophrys and Ciliata.

The green color of the water in the pools is due to the presence of an abundance of green algae, chiefly Chlamydomonae, and the brownish tinge is caused by the increase of diatoms, namely, some species of Navicula and its allies. These are the two most prominent forms of plant life in the pools.

As before stated, pools I and II were formed later than the others, and their water remains clear all the time; accordingly in them the biological content is more meager, consisting of a small number of Navicula, Chlamydomonae, and one or two ciliated protozoa. In late summer, however, a noticeable change takes place. At the bottom of these pools a thin layer of brownish organic matter is formed, largely made up of Navicula with comparatively few Chlamydomonae. This deposit does not affect the transparency of the fresh brine water.

Owing to the wide area and exposed surfaces which are easily reached by sunshine, thick, foamy, brown scums are found here and there on the surface of the shallow water in the overflowed areas. These scums afford the larvae, especially during early stages, shelter and shade when the sun's rays at noontime are too strong; they act as a moisture retainer when the areas are rapidly drying up; and finally, for the larva as well as the adult, they constitute a main source of food supply. These floating scum masses embody the entire fauna and flora in the shallow water.

In comparing the two sets of pools—A to F, and I and II and the overflowed areas—it was found that in the former group green algae predominated, with the protozoa more numerous, while in the latter group the brown algae were in greater abundance.

LIFE HISTORY

THE LARVA

Morphology

Various methods were tried for studying the anatomy of the larva. The following methods yielded the most satisfactory results.

For the muscular system, it was found that specimens were best fixed in slightly warm Bouin's or Gilson's solution. Both the cutaneous and the cephalopharyngeal musculatures appeared opaque white, and were thus to be distinguished from other structures. For the nervous, alimentary, tracheal, and vascular systems and the imaginal disks, 10-per-cent formalin seemed best. The fine branches of the nerves and tracheae were preserved intact and were recognized and distinguished from one another under a binocular microscope with the aid of bright sunlight or the artificial light of a nitrogen-filled lamp. The imaginal disks were best studied by staining with diluted methylene blue (5 drops to 5 cubic centimeters of water); this distinguished them from the nervous ganglions, which do not take the stain to the same degree. The dorsal vessel, the ring, and the entire alimentary system were preserved in perfect condition in this weak fluid. In checking up the gross dissections, serial sections were cut from 5 to 10μ with a microtome. Here again Bouin's and Gilson's solutions were the fixers used. The following was the procedure: Certain parts not to be studied were snipped off in order that the fixer might penetrate quickly. The specimen was killed in hot solution and fixed for from 12 to 24 hours, washed in 85-per-cent alcohol which was changed three or four times a day, and stained *in toto* in borax carmine for from 24 to 48 hours. The specimen was then de-stained in 70-per-cent acidulated alcohol for from 12 to 24 hours, in 85-per-cent alcohol for 24 hours, in 95-per-cent alcohol for 24 hours, in absolute alcohol and cedar oil for 24 hours, in cedar oil for 24 hours, in 56° paraffin for 24 hours; section from 5 to 10μ; xylene 5 minutes; in 95-per-cent alcohol 5 minutes; in carbol-xylene for 5 minutes. Lastly, the specimen was mounted in balsam.

External features

General features. The body of the larva consists of twelve segments. The first, or head, segment is often retracted and not visible from

above. The second, or first thoracic, segment is partly retracted and a pair of sense papillae are visible both laterally and ventrally. Owing to the retraction of these two segments, there results an oval opening or invagination, bordered by the fold of the integument of the first thoracic segment, situated cephalo-ventrad at the anterior end of the larva. In the specimens fixed in Bouin's or Gilson's solutions, the wrinkles in the integument are flattened out, and the first two segments are stretched and distended, so that they can be easily examined; but the segments throughout the whole body are not very distinct externally.

The shape of the body is more or less cylindrical. The body tapers off gradually from the third segment toward the anterior end, while the diameter increases from the twelfth segment toward the posterior end; but for the most part the diameter of the abdominal segments is fairly uniform. The caudal process is circular in cross section and terminates with a more or less truncate end, where two cylindrical branches arise. Through these branches the main trunks of the tracheal system come to the exterior. The average length of the full-grown larva (Plate LIV, 2), including the caudal process with its branches, is 12 millimeters.

The integument.— In the young larva the integument is grayish in color, and is thin and more or less transparent, so that some of the internal organs can be seen through the skin. The body is more or less hairy. In the mature larva the hairs on the dorsum are more pronounced than those on other parts of the body. On the dorsum are seven somewhat V-shaped blotches, the hairs of which are modified into flat scales. The prothoracic segment is covered with short and blunt bristles.

In cross section the cuticular integument is composed of two layers The outer layer is thin and slightly chitinous, bearing the chitinous hairs, while the inner layer is very thick and homogeneous in structure. Underneath the two layers is a thin layer of hypodermis. The writer has never been able to see the hexagonal cells of the hypodermis as mentioned by Trägårdh (1903). However, the large oval nuclei of these cells are very conspicuous.

The appendages.— The very short antennae, each consisting of two joints, are above the prominent oval lobes and are scarcely visible at all when the head is retracted. A pair of chitinous prothoracic stigmas, each consisting of four digits, are borne one on each side in the second segment. The stigmas are ordinarily visible, but sometimes, by the

retraction, of the first two segments, they are entirely concealed within the fold of the integument. The thoracic segments are footless, while each abdominal segment bears a pair of prolegs. These prolegs are nipple-shaped, are fused at the basal third, and bear a number of claws on their blunt tips. These claws are arranged in three rows, usually with five in the first, four in the second, and four or five in the third. The number varies and the size of the claws decreases row by row. In addition, there is one more row of rather insignificant small claws. The last pair of prolegs are more prominent than any of the preceding ones, and the claws upon them are much larger. The claws here are opposed in position to those on the other prolegs. This enables the larva to grasp an object by means of these and the two preceding pairs, when pupation is impending.

Behind the anal opening is a pair of more or less rounded pads which are considered as parts of the prolegs, and a number of small claws are borne on them. The caudal process is a cylindrical sheath, into which its two branches can be withdrawn. It is longer than any segment in the body of the larva, being about three or four times as long as the twelfth segment. At the end of each branch of the process is a chitinous cap with one large round pit situated at the center and four small openings on a chitinous knob surrounding this pit. At the inner border of each of these openings is attached a fan-shaped thin membrane, which can be seen best when the larva sticks its caudal tips to the surface of the water for respiration (Plate LIV, 7).

Internal structures

The tracheal system.— The tracheal system consists mainly of two pairs of longitudinal trunks, one dorsal and one ventral. The dorsal trunks are large and are the true trunks, while the ventral are more delicate and are made up merely by the connection of the outer branches of the dorsal pair (Plate LIV, 8). The dorsal pair begins in the second segment where the prothoracic stigmas open out through the body wall, and extends posteriorly to the caudal tips, which bear the spiracles. Connecting these two main trunks in the fourth segment is a commissure, overlying the cephalopharyngeal skeleton. Trägårdh states that in *Ephydra riparia* this is the only commissure, but the writer has found in *Ephydra subopaca*, in the caudal region close behind the twelfth segment, a very short commissure concealed by the crossing of the two tracheal trunks.

In addition to the two just mentioned, another one is found in the ninth segment. This commissure, however, is not so large as the anterior one and it might easily be confused with some of the inner branches from the trunks.

As the larva is amphipneustic, each dorsal trunk has its anterior and its dorsal spiracles. The anterior spiracles are lacking in the young larva during the first instar. The anterior spiracular process consists of a hand-shaped body bearing four digits, although sometimes only three are present. Each digit has a small opening at the tip (Plate LIV, 6). The posterior spiracles are found in the larva shortly after hatching. At this time, the caudal process, however, is not well developed. At the caudal end there appear two oval disks (Plate LIV, 4), which become the tips of the future caudal branches. In the center of each disk are two metallic shining chitinous knobs with a small round pit closely mesad to each of them. The spiracles are in the center of these knobs. When the larva is mature, the flat disk develops into a conical cap and each of the knobs breaks up into two parts, thus making four all together on each cap surrounding a large round pit in the center. There are four curved grooves around these knobs (Plate LIV, 7), distinctly delimiting the discontinuation of the chitin at the tip of the cap. The central pit is bordered with four fan-shaped chitinous membranes which Trägårdh calls "chitin blätter." These membranes are outspread when the caudal tips come to the surface for breathing, but each becomes folded longitudinally to cover over its spiracle when immersed.

Each dorsal trunk has eight pairs of inner branches and ten pairs of outer branches. The former are smaller than the latter. The branches of the first pair at the fourth body segment of the larva attach to each side of the cephalopharyngeal skeleton and there ramify. The branches of the second pair originate in the same segment, and shortly after their origin each branch divides into an anterior and a posterior sub-branch, the former going to the cephalopharyngeal mass, the latter to the ring. The third and fourth pairs are found in the fifth and sixth segments, respectively, overlying and supplying the proventriculus. Branches in each of these two pairs meet each other and are conjoined at their tips, thus resembling a commissure. Following this are the fifth and sixth pairs in the sixth and seventh segments, respectively. These supply the posterior part of the proventriculus. The seventh pair lies in the eighth

segment, and, as with the third and fourth pairs, the tip of each branch from one side meets its fellow from the other to form a false commissure. Finally, in the tenth segment is the eighth pair. Both this pair and the preceding one supply the convoluted mid-intestine.

Of the outer branches, those of the first pair arise in the fourth segment. They turn inward, extend forward as far as the first segment, and divide into several branches there to supply the muscles of the cephalopharyngeal skeleton. In the fifth and sixth segments arise, respectively, the second and third pairs, which supply the imaginal disks of the wings, halteres, and mesothorax. These branches divide into sub-branches. The sub-branches of the second pair go to the third segment and end underneath the cephalopharyngeal skeleton, either with or without further ramification. The sub-branches of the third pair are connected with different structures within the body cavity. One of the sub-branches of this pair connects with corresponding tracheal branches of other segments to form the slender ventral trunk. From the fourth pair to the eighth, inclusive, each branch consists of four sub-branches, one arising from the dorsal trunk, one going to the ventral trunk, one penetrating the fat bodies and ending in the dorsal body wall, and one passing mesad underneath the dorsal trunk and supplying the alimentary canal. In the sixth pair there is a prominent white tracheal body in each inward-turning sub-branch. The function of these bodies is perhaps hydrostatic. The ninth pair is similar to any of the preceding ones, except that one of the sub-branches, instead of attaching to the alimentary canal, goes to the lateral body wall. The branches of the tenth pair are very strongly developed. They arise in the caudal process and extend forward as far as the eighth segment, to connect with the alimentary canal. Each branch has two large sub-branches, one anterior and one posterior. The anterior sub-branch goes to the eleventh segment and is attached to the hind intestine. The posterior sub-branch subdivides itself again, sending out an anterior sub-branch to supply the twelfth segment and a posterior sub branch to extend to the end of the caudal process. The strong development of the last pair of the outer branches, as Trägårdh considers, is due to the elongation of the hind intestine, but, in addition to this, the writer is inclined to think that the elongation of the caudal process, when the larva grows, must be a cause also.

In the dorsal trunk taenidia are present in the parts anterior to the first outer branch and posterior to the sixth outer branch. These parts are distinguished from the rest by the dark brown color. In the parts where taenidia are absent the color of the tracheal trunk is silvery white. There is an absence of taenidia in four places in each trunk, three of which are close behind the sixth, seventh, and eighth outer branches, respectively, and one is between the ninth and tenth outer branches.

As already mentioned, the ventral trunks are a secondary make-up through the connection of the sub-branches from the dorsal trunks, so they are much more slender and delicate than the dorsal. In each trunk the anterior end ramifies in the fourth segment underneath the cephalopharyngeal skeleton. From the fifth to the eleventh segment, inclusive, there is an inner branch in each segment. This inner branch ramifies in the prolegs. In the twelfth segment the anterior end of the trunk ends with the alimentary canal. The ventral trunk has two outer branches in each segment from the fifth to the tenth, inclusive. All of them go to the latero-dorsal body wall (Plate LIV, 8 and 9).

The fine branches that penetrate the subesophageal ganglion are connected with the ventral trunk. Such connection can be best seen from the lateral aspect, when the specimen is fresh and the trachea are filled with air.

The nervous system.— The nervous system of this form in general differs very little from that of the larva of Musca. The nervous center consists of a boat-shaped ganglion and two prominent cerebral lobes. Between the latter pass the esophagus, a pair of tracheae, and the dorsal vessel. Cephalad to the lobes are two major cephalic imaginal discs, each of which is connected antero-laterally with an optic stalk. The only difference here from the larva of *Musca domestica* is that there is no such problematical cellular structure as was figured by Hewitt (1908), situated close above the major cephalic disks and the cerebral lobes (Plate LIV, 10).

The nerve branches I and II arise from the cephalic part of the central ganglion, one of them (I) going to the cephalopharyngeal mass, and the other (II) going to the muscles of the lateral pharyngeal sclerites. There are three pairs of nerve branches (a, b, and c) arising from the stalks of the prothoracic and mesothoracic disks. In addition to these, nine pairs arise from the lateral and caudal parts of the ganglion. From

the posterior half of the central ganglion arise three unpaired accessory nerves which are much finer than the others. Except in the first four branches (I, II, a, and b) the bifurcations of these nerves are very similar to that in the Musca larva, while in innervation there is practically no difference between these two forms (Plate LV, 13). Each of the fourteen paired nerve branches is associated with a trachea (Plate LIV, 10). The penetration through the ganglionic sheath by the trachea gives a metallic luster along the edge of the ganglion.

There are two prominent pairs of sense organs in the head region. The anterior pair is on the antennae and the posterior pair is on the maxillary palpi (Plate LIV, 2). The palpi are shorter than the antennae, are not jointed, and have a broader base. The innervation of the former comes from the subesophageal ganglion (Trägårdh), that of the latter from the cephalopharyngeal mass. On the dorsal and lateral parts of the thorax, and along the lateral of the entire abdomen, parallel to the main tracheal trunks are papillae of another type which are much more slender, with a cylindrical stem. At the tip of the stem branch are three or four tentacles. These have been figured by Trägårdh (1903). The nerve ganglia lie close above the upper pharyngeal plate. They are fused anteriorly but clearly separated from each other behind. These are the epipharyngeal ganglia. Just opposite to them, on the ventral side of the pharynx, are the hypopharyngeal ganglia. These two pairs are best seen in cross sections.

The muscular system.— The muscles, aside from those of the alimentary and vascular tracts, are in two main groups—one controlling the cephalopharyngeal region, the other constituting a part of the body wall. It is these two main groups of muscles which are herein discussed.

The cephalopharyngeal muscles.— In the cephalopharyngeal region the muscles are very similar to those found in the larva of Musca. Starting from the cephalic end, a pair of mandibular extensors is seen, inserted on the dorsal side of the mandibular sclerites. The attachment of these muscles is made to the dorsal body wall of the third segment Caudad to these another pair of muscles is inserted on the dental sclerites. These are the mandibular depressors. The other end of this pair on each side is divided into three bands and attached to the ventral process of the lateral pharyngeal plate. On the hypostomal sclerites are inserted four pairs of muscles, two dorsal and two ventral. The dorsal pairs are attached

to the intersegmental ring of the third and fourth segments, while the ventral pairs are attached, one to the caudal end of the dorsal process of the pharyngeal plate, and the other to the ventral. They are stomal dilators. The pharyngeal depressors are the pair of muscles situated dorsal to all the others. They have one end attached to the intersegmental ring between segments 3 and 4, and the other end inserted on the posterior end of the dorsal side of the pharyngeal mass. There are two pairs of cephalopharyngeal protectors, one dorsal and one ventral. These are attached to the third segment of both the dorsal and the ventral side, respectively. Their other ends at each side are inserted together on the dorso-lateral region of the posterior end of the pharyngeal mass. Six pairs of cephalic retractors are inserted into the cephalic ring between the first and the second segment. The three dorsal pairs are attached to the posterior end of the fourth segment, while the three ventral pairs, attached to the same segment, are slightly cephalad in position.

Within the pharyngeal mass there are two sets of muscles, which are best seen in sections. One set is longitudinal. Hewitt, in the Musca larva, calls them the *oblique pharyngeal muscles*, because their ventral attachment is posterior to the dorsal attachment. These muscles are attached dorsally to the inside of the dorsal ridges of the lateral plate and ventrally to the roof of the pharynx. The other set is best seen in the caudal region of the pharynx. They lie horizontally over the pharyngeal cavity, and are called by Hewitt the *semicircular pharyngeal muscles* (Plate LV, 20).

The cutaneous muscles.— On the inner side of the dorsal body wall, two pairs of the dorsal longitudinal muscles are found, lying on both sides of the median line. They are arranged according to the body segments. On the ventral side there are three pairs of ventral longitudinal muscles. Both the dorsal and the ventral sets are the most prominent muscles of the body wall. Between each two segments, from the fourth to the twelfth inclusive, a more or less spindle-shaped muscular band, called the *intersegmental muscle*, touches both the dorsal and the ventral longitudinal muscles. There are two pairs of lateral longitudinal muscles on both sides which extend from the third segment to the twelfth. The more ventral muscle on each side comes anteriorly into contact with the cephalic retractor in the fourth and fifth segments but turns away before it terminates near the demi-annular muscles in the second segment, while

the more dorsal muscle comes anteriorly to the third segment and ends almost in the same region as does the ventral muscle. All these muscles in the two pairs come posteriorly into contact with the ventral longitudinal at the posterior end of the twelfth segment. The oblique muscles are separated in each segment, from the fourth to the twelfth. In each segment there are three pairs of internal dorso-lateral oblique muscles and three pairs of external muscles. Likewise, there are both internal and external ventro-lateral oblique muscles, but only one pair of each. Two pairs of internal ventral oblique muscles and one pair of external ventral oblique muscles are found in each abdominal segment except the twelfth. The demi-annular muscles are found in each segment. There are four pairs in segments 5 to 11, inclusive, while in the other segments the number varies. In the last segments the muscles that are connected with the anal lobes are the anal muscles (Plate LVI, 31 and 32).

The alimentary system.— The alimentary system consists of the tract and its appendages. The alimentary tract in the mature larva is about three times as long as the entire body. The different parts of the tract are distinctly marked out by constrictions or by the insertions of the appendages.

The mouth opens ventrally at the anterior end, bordered by two oval lobes. The mandibular sclerites are exposed, each bearing a series of "teeth" resembling a comb. The hyposternal sclerites are set posteriorly inside the oval cavity, but they are invisible through the semi-transparent skin. Four pairs of large chitinous tubercles are arranged in two series close beside the oval cavity, and lateral to them are four series of smaller ones. Their size increases to the last row. At the farthest cephalo-dorsal position are four large tubercles, two on each side of the median line, and still dorsad to these, another four large ones are found close to one another in a row, resembling the premaxillary teeth of the mammals (Plate LV, 15).

The cephalopharyngeal skeleton.— In the second instar the "skeleton" is very slender. The mandibular sclerite consists of a single piece, more or less U-shaped and with a series of teeth, while another single piece composes the remainder of the skeleton. These two pieces of the whole skeleton are rather apart from each other but joined with each other through muscles. As the larva matures, the U-shaped piece breaks into two pieces. Dorso-caudad of them are a pair of dental sclerites and a pair of slender chitinous plates. A pair of hypostomal sclerites are

separated from the rest of the skeleton. These sclerites are connected ventrally by a hypopharyngeal sclerite. The rest of the skeleton is divided into dorsal and ventral lateral plates. Each has a caudal process projecting posteriorly. The dorsal and ventral plates are connected with a dorso-ventrad piece, making an I-shaped outline (Plate LV, 19). At the anterior end of the dorsal plate lies the epipharyngeal sclerite. The caudal part of the ventral lateral plate is broad but gradually thins away. Near the dorsal angular border of this plate an oval opening is often found.

The pharynx, as in the larva of Musca, has eight grooves separated by the bifurcating ribs at its floor. These ribs, differing from those found in the Musca larva, are rather Y-shaped, with fine comb structures at the tips of the upper processes. This evidently suggests a straining function. The loose membrane attached to the layer of cells covering the lateral plate, found by Hewitt in the Musca larva, is also found here (Plate LV, 19).

The esophagus is uniform in diameter throughout its length. It passes through the foramen between the cerebral lobes and the subesophageal ganglion, leading posteriorly to the proventriculus (Plate LV, 14), with which it communicates by means of the esophageal valve.

The proventriculus has very thick epithelium and its shape is more or less oval. As the posterior esophagus telescopes into the central core of the proventriculus, the large, clear cells of the proventriculus surround this inserted part. At the anterior part of the proventriculus and at the posterior end of the esophagus the epithelial cells are very large.

The chyle stomach may be divided into two parts. The narrow anterior part is the ventriculus, while the broader posterior part is the mid-intestine. The convolution of the chyle stomach is very complex. The anterior end, where the four caeca arise, is the broadest part in the entire alimentary canal. The epithelial cells of the ventriculus are large. The striated appearance, as in the other dipterous larva, is found on the sides of cells facing the lumen. The mid-intestine has a very thin epithelium and the wall of this part in the alimentary canal is almost transparent. The lumen, of course, is much larger than in the ventriculus (Plate LVI, 25).

The hind intestine begins with a very narrow part, then it broadens, but as a whole it is much narrower than the chyle stomach. It curves immediately after it commences, at the place where the malpighian tubes

arise, and then runs posteriorly toward the last segment. The epithelium in this part becomes thick again. At the tenth and eleventh segments it becomes narrower, and then begins the rectum (Plate LV, 14). The rectum has a very thick muscular wall. The chitinous intima is thick. As the anal opening is ventral in the twelfth segment, the position of the rectum is almost vertical.

The appendages of the alimentary canal.— The salivary glands are large and tubular. Each one has a narrow duct leading to the pharyngeal mass, under which the two ducts unite into one. This common duct leads forward and opens into the pharynx (Plate LV, 14).

The four caeca, attached immediately behind the proventriculus, have a broad base and each is glandular in appearance (Plate LV, 14).

The malpighian tubes are very large and often twisted among the convolutions of the alimentary canal and the large fat bodies in the abdominal region. There are two pairs, and each pair has a common root inserted at each side of the end of the mid-intestine. The tubes consist of large cells with prominent nuclei (Plate LVI, 26).

The vascular system.— The dorsal vessel consists of the heart, which is posterior, and the aorta, which leads anteriorly from the heart. This vessel lies immediately beneath the skin and above the alimentary canal and the four large fat bodies. The heart is the swollen and enlarged part lying in the last four segments. The anterior end of the dorsal aorta is between the cerebral lobes of the brain. The heart has three pairs of ostia situated latero-dorsad. They are furnished with valves which lead from the body cavity into the heart. Immediately at the anterior end of the heart there is another pair of valvular flaps regulating the flow of blood into the dorsal aorta. Along the sides of the heart and attached to the ventral side of it are three pairs of wings. Each wing has its narrow tip connected to the lateral body wall. The pericardium, which forms a narrow sheet along each side of the dorsal vessel, extends through the entire length of the heart and a part of the aorta. The extension can be readily recognized through the large epithelial pericardial cells. These cells are arranged one after another at short intervals along the dorsal vessel. The muscles in the wall of the dorsal vessel are arranged transversely and longitudinally, but chiefly in the latter direction in the aorta, and almost exclusively in the heart. At the posterior end of the heart extend three more wings, two lateral and

one dorsal; the dorsal wing is attached to the dorsal body wall, while the two lateral wings are attached to the lateral body wall. These wings are, however, smaller. The pericardium is profusely supplied with tracheae (Plate LVI, 33), as has been found in other dipterous larvae, such as Musca, Calliphora, Psychoda, and Anopheles.

The reproductive system.—In the mature larva a pair of gonads is found in the fifth abdominal segment. They are imbedded in the fat bodies and each has its duct leading posteriorly to the ventral body wall. They are pyriform, and at the posterior end there is an accumulation of imaginal disks. The general arrangement of cells in the gonads (Plate LVI, 34) is similar to that described by Weismann (1864) in the larva of *Musca vomitoria*, and according to his description these gonads are a pair of testes.

The imaginal disks.— The imaginal disks in the larva are of two kinds, the paired and the unpaired. The latter are insignificant and developed later, while the former are prominent and perfect in shape as soon as the larva enters the third instar. The unpaired disks are found in the alimentary canal and in the hypodermis, and they have to do with the development of the future fly. The writer has not been able to find the hypodermal rudiments in his preparations, because they are developed after pupation commences. Those scattered in the alimentary canal are similar in shape to those found in the larva of Musca. They are located at the anterior end of the proventriculus, all over the mid-intestine, behind the base of the malpighian tubes, surrounding the anus, and at the anterior end of the salivary glands, as figured by Kowalevsky (Plate LV, 14). The paired disks may be again divided into two groups according to their locations, namely, the cephalothoracic and the abdominal disks.

The cephalothoracic disks.— There are eleven pairs of disks in this region. They are the centers of development for the different parts of the imaginal head and thorax, and their appendages. Closely adjacent to the cerebral lobes is the pair of optic disks, which are connected with the lobes through the optic stalks. The optic disks are applied to the front of the lobes with their posterior concave surface, while their anterior convex surface is connected with a stalk leading to the antennal and frontal disks. The two pairs can be distinguished in sections. The antennal disks, more or less elliptical in outline, lying between the optic disks and the cephalopharyngeal skeleton, terminate in elongated stalks,

leading cephalad to the pharyngeal skeleton (Plate LVII, 35). Ventrad to these two pairs just mentioned are two other pairs; the pair situated near the central ganglion are the mesothoracic disks, which will be developed as the mesothorax and the middle pair of legs, while the other pair anterior to them are the prothoracic disks for the prothorax and the anterior legs (Plate LVII, 36). These latter two pairs are similar in shape to each other, each having an elongated stalk leading out forward and connected with the ventral hypodermis. There are four pairs of disks on the dorsal tracheal trunks (Plate LVII, 37). In each trunk close behind the prothoracic stigma is the stalkless, and more or less bean-shaped, pronotal disk embracing the tracheal stem (Plate LIV, 6). In the fourth segment is a disk, the largest of all, known as the *mesonotal and wing disk*. This disk is somewhat pear-shaped, is connected with the tracheal trunk, and has its stalk leading forward. Mesad and ventrad to this are two smaller disks. The anterior one is the mesothoracic disk, and the posterior is the metanotal and the haltere (Plate LVII, 38). To the external side of the hypostomal sclerite is attached an oval disk (Plate LVII, 37), and another is attached to the internal side of the sclerite. The former is the proboscis disk, and the latter the pharyngeal, which can be best seen in sections. Hewitt maintains that the maxillary disks are small and flask-shaped, and are found at the base of the oval lobes, but the writer is inclined to think these are probably a pair of sense organs.

The abdominal disks.—Closely ventrad to the rectum is a pair of pear-shaped disks which have been considered as the rudiments of the external genital appendages. Differing from what has been found by Künkel d'Herculais (1875) in Volucella, the other pair is absent (Plate LVII, 37).

The peripodal membrane is thin and transparent. When pupation commences, the differentiation of these rudiments can be seen through this delicate envelope. Each of the stalked disks has a nerve branch and a fine trachea. The parts that are sheathed within the peripodal membrane can be readily recognized (Plate LVII, 39 and 40).

Growth

Molting

While making observations on the development of the larva after hatching, molting has frequently been noticed. As soon as the young larva attains its size, about three millimeters in length, the skin splits

longitudinally along the dorsum of the second and third segments, and through this dorsal opening emerges the head of the larva of the next instar. The rent here may become much enlarged, extending backward as far as the sixth segment, while the larva is struggling for liberation. It seems that the larva does not encounter much difficulty in slipping out of the old skin. Because of its cylindrical body and short prolegs its escape is easy. Sometimes, however, the last pair of prolegs causes a great deal of trouble. These prolegs are often caught on the cast skin with their claws. After a struggle, lasting sometimes for half an hour, when the caudal processes have been pulled out, these remain still entangled with the cast skin. The larva, as it has sometimes been observed, twisting and bending its body, uses its mouth parts to bite this off. In the exuviae are found the entire cephalopharyngeal skeleton, part of the alimentary tube, and the tracheal trunks from out the caudal processes.

The writer did not observe the second molting. A premature molting may be caused by subjecting the larva to certain abnormal conditions, as once it was done by accidentally dropping larvae in kerosene. Such a molt, however, is quite different from an ordinary ecdysis; it consists of nothing more than the primary cuticula, and the structures that are cast off sometimes with the ecdysis are not to be found in it.

Instars

The first instar.— The newly hatched larva measures from 1 to 1.5 millimeters in length. The body segments are very distinct but the caudal processes are just budding out. At their blunt end are chiefly visible the tracheal terminals. These terminals are much simpler than those found in a grown larva, each having an opening, laterad to which are two roughly outlined bullae. Of the anterior spiracular processes there is not a trace to be recognized during this stage. The cephalopharyngeal skeleton is delicate and slender in shape, consisting, at the anterior end, of a single piece of U-shaped mandible sclerite and, following this, a pair of H-shaped structures, representing the hypostomal sclerites in front and the lateral pharyngeal plates posteriorly. The mandible sclerite and the rest of the cephalopharyngeal skeleton are apart from each other, but they are connected and articulated with each other by muscles. The alimentary canal is a more or less straight tube and

the salivary glands are relatively large. This stage lasts from four to five days at a room temperature of from 23° to 35° C.

The second instar.— At this time the larva is provided with a pair of pale, slender, anterior spiracular processes, the digits of which are short and not distinct. The posterior spiracles have assumed the general shape that they will have in a full-grown larva, but are smaller in size. Each of them has a chitinous cap with an opening at the center, surrounding which are four tubercles. The cephalopharyngeal skeleton is much thicker and heavier than in the preceding stage, and the hypostomal sclerite is now a separate piece from the lateral pharyngeal plate. This stage lasts about four days at a temperature of from 25° to 28° C.

The third instar.— The larva has attained its maximum size of from 12 to 13 millimeters in length. The difference in body structure has been described under *Morphology*, page 567. The larva completes its development and pupates in the course of three or four days at a temperature of from 29° to 30° C. Sometimes under less favorable conditions this stage may extend over a period of about a week.

Observations on growth in salt and fresh water

The following experiments were performed in the laboratory. Each aquarium was 5.5 centimeters in diameter and contained water, salt and fresh, with a depth of about 1.25 centimeters. Water and food materials were added whenever necessary. The aquaria were in series, placed near a window and carefully guarded against dirt and accident.

Experiment I.— Three larvae, each of which measured from 2 to 2.5 millimeters in length, were placed in salt water. After four days they measured 5 millimeters each; after five days one of them measured about 7 millimeters and the other two about 6 millimeters; after seven days the largest one measured 9 millimeters; after eleven days the largest larva pupated, while the other two measured 9 and 7 millimeters, respectively; two days later the remaining two larvae pupated. The room temperature ranged from 23° to 29° C.

Experiment II.— Three larvae of the same size as those used in Experiment I were placed in fresh water. After four days each one measured about 4 millimeters; after five days they averaged from 4.5 to 5.5 millimeters in length; after seven days one measured 7 millimeters and died, while the other two measured about 6.5 millimeters on the tenth day

and died. The average room temperature was the same as that in Experiment I.

Experiment III.— Four eggs were placed in salt water. After one day one of them hatched and the larva measured 1 to 1.5 millimeters; later on the same date the remaining three eggs hatched and on the fifth day the larvae averaged from 4 to 5 millimeters in length; after seven days they averaged from 7 to 8 millimeters; after eleven days one larva measured 10 millimeters, a second one measured 9 millimeters, and the other two measured from 8 to 9 millimeters and at this time pupated. On the thirteenth day the other two pupated. The average room temperature was the same as that used in Experiments I and II.

Experiment IV.— Four eggs from two to three days old were placed in fresh water. After one day two of them hatched; after four days these two larvae measured from 2 to 2.5 millimeters each; after five days one measured 3 millimeters, and the other 4 millimeters; after seven days the other larvae, which hatched out much later, averaged 2.5 millimeters each; the one which measured 4 millimeters on the fifth day died. All the others died on the thirteenth day. The average room temperature was the same as that in the first three experiments.

In a comparison of the results of the above experiments, the striking difference in the development of the larvae in the fresh and in the salt water may at once be seen. None of the larvae could grow well and attain pupation in the fresh water with the total absence of salt, although other conditions were equal. The larval stage in salt water, under the conditions previously stated, lasted from eleven to thirteen days. The pupation took place much earlier than usual, when the larva was only from 8 to 9 millimeters long. This was, perhaps, due to the more even temperature or other artificial conditions maintained in the laboratory.

Habits

Locomotion

The larvae are always found in still and stagnant water. Their modes of locomotion, under normal conditions, show their adaptation to such environments. First of all, the larvae are slow in movement, never darting nor jumping with appreciable speed; in the second place, they are awkward in directing themselves forward and turning themselves around, never exhibiting any energetic directness. And finally, the larvae, especially when reaching maturity, prefer to remain still on

rocks, logs, or floating leaves near the surface for a considerable length of time, without attempting to make a change in place unless compelled. The locomotion may be classified into four modes.

Crawling.— As the body is more or less cylindrical and smooth, and not equipped with specialized organs for swimming, the larva crawls most of the time at the bottom or on some object floating in water. Its prolegs, although short, are equipped with well-developed claws for such a purpose. In the summer season, when it is cloudy, a number of larvae are often found crawling slowly on floating logs in the pools or on the soft mud bottom in the shallow, seldom disturbed water of the overflowed areas. The larva, in its way of progression, much resembles a caterpillar, only that its prolonged caudal process is held upward like a cat's tail, waving around, and sometimes even bending forward to touch upon the dorsum. Under bright sunshine, by the sudden brushing away of the floating scums, the larvae hiding in the shade beneath are put to "flight"; however sluggish they seemed, they now begin to crawl faster, showing uneasiness under the suddenly changed conditions. This, of course, can only be attributed to the effect of light, which will be discussed later. The larvae — most of them mature — have been found crawling on floating scums. In the laboratory aquarium the writer has seen a young larva crawl into an algal mass, become trapped with the filaments, and then struggle for freedom; being tangled with algae on the claws of its proleg, the larva was deprived of liberty, yet, because there was abundant food material in such a mass, it probably did not die, but attained maturity.

Swimming by means of wriggling.— Wriggling is another mode of locomotion generally employed by the larva. The body of the larva is not slender, consequently its wriggling is not so rapid and vigorous as that in some other aquatic dipterous larvae. But this larva, nevertheless, bends and twists itself freely in all directions. Its caudal process, naturally, is the most flexible part, whipping and lashing around to help in locomotion. It wriggles sometimes near the surface, sometimes near the bottom, or sometimes between the surface and the bottom, in no definite direction; but more frequently it ascends and descends in the water. After a shower or in the late afternoon of a clear day, a number of the larvae may be seen wriggling very slowly, each with one side of the body upward about an inch below the surface in open water. In wriggling, as well as in crawling, two or more larvae sometimes hold together by

means of the last pair of prolegs, or with the prolegs of one on another part of the other, entangled and struggling aimlessly.

Floating.— The larva often floats itself up to the surface. The larva does not necessarily touch the surface, but often stays about an inch below. Usually, when floating, the larva has its head pointing obliquely upward and its body held, bending or straight, in a somewhat horizontal position. However, there is no definite rule as to its position.

Dropping.— Dropping may take place after wriggling, after staying below the surface for a considerable time, or immediately after floating. Sometimes the larva, instead of holding its head obliquely upward as it often does, reverses the process in making its way downward. In pools I and II, where the water is clear, this mode of locomotion can be best observed when the larva is getting near the bottom. Its body seldom touches the bottom, for at some point within an inch from the ground the larva will stop dropping and remain stationary. Sometimes wriggling may be assumed at this moment. Likewise, wriggling may also break in midway in dropping, so this mode of locomotion is likely to be interrupted almost anywhere before the end of the descent is approached

Feeding

Method of feeding.— The larva often crawls on the surface of floating leaves and stops there to feed. Its mandibular sclerites move rapidly, bending back and forth. The head segment is extended and moves with frequency, corresponding to the movement of the cephalopharyngeal skeleton. The mouth parts graze vigorously on the materials deposited on the plant surface, and the tooth-like structures on the ventral side of the distal part of the mandibular sclerites comb up the desirable materials. As the larva seldom feeds long on one spot, its head swings freely in all directions seeking a new feeding place. While the larva is feeding at the surface of open water, the ventral side of the first segment, including the mouth, is flatly applied to the surface film. The continuity of the latter is frequently disturbed by the vibration of the oral lobes. These lobes with their chitinous tubercles serve as a sort of brush in producing little whirling currents, in which the microscopic organisms are involved and brought to the mouth. Meantime the inner, more prominent tubercles, which are situated close to the oral cavity, sweep simultaneously toward the center. The mandibular and dental sclerites move forward to meet the flowing currents, and repeatedly relax and fall

back. This movement is carried on with great frequency, about two hundred times a minute. The current, which carries food materials into the alimentary canal, can be seen through the semi-transparent skin. A number of air bubbles move along in the convoluted tract. The larva also crawls in the dirt at the bottom, picking up food materials from the bottom surface and selecting them from within the mud.

Selection of food.— The food of the larva consists, in the main, of microscopic organisms living in the salt water. The green and yellow tinge in the pools, and the brown scums in the overflowed areas, are the chief natural sources from which the larva selects its food. Aldrich thinks that an alga of the Nostoc group, which is common everywhere in Great Salt Lake, often forming rotting deposits, must be the food of the Ephydra group. In the pools where these observations were made, no Nostocs have ever been found, but algae of other groups, green and brown, are found in considerable quantity. In the old pools, in which there is now very little salt, masses of Ulothrix float in the water. These plants probably furnish both shelter and food for the larvae. Evidently the larvae do not live on one particular kind of plant material. Besides algae, some decayed leaves, fragments of decayed grass stems, boards or logs, even some microscopic animals, such as Protozoa and bacteria, may be consumed by the larvae. Besides organic food, some inorganic substances, although undesirable, may get in the alimentary canal, without being digested. In studying the food selected by the larvae, twenty alimentary canals have been dissected and examined in the field under the microscope, and also in the laboratory immediately after the specimens were brought in. The materials constituting the stomach contents, that are recognizable and identifiable, are listed as follows:

	Specimens																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Cinders			c						vc	s	c			c	c	c	c		c	c
Iron rust			c	c		c			vc	s	c			c	c	c	c		c	
Bacteria																				
Pandorina												vs					c			
Vorticella										s										
Mastigophora			c																	
Gloeocystis									s											
Astasia																				
Intusoria																				s
Synedra	s																			
Chlamydomonas	c	c	c	c	c	c	c		c	s	s			c	c	c	s			s
Navicula	vc	c	c	c	c	c	c	c	vc	vc	vc	c	c	c	c	c	vc	vc	vc	vc

c, Common, vc, very common, s, scarce

In addition to the natural materials selected by the larvae, different kinds of foreign food — foods not found in their natural habitat — were used to learn what kind of plant materials would serve as the most favorable food to them. The water taken from the pools was filtered in order to eliminate any natural food. The four kinds of foreign food — (1) cornmeal, (2) green grass, (3) broad leaf plantain, and (4) alfalfa meal—were placed respectively in four aquaria. Each aquarium had five larvae measuring from 7 to 8 millimeters in length. After five days the larvae in the first two aquaria all died. After two weeks, two pupae were found in each of the other two aquaria. At the end of three weeks, three adults and one pupa were found in the fourth aquarium with the alfalfa meal in the water.

Respiration

In respiration the larva sticks out its caudal process to indent the surface film. The spiracle membranes flatten out on the water surface, resembling the leaves of Marsilea, and the spiracles open to the air. Meanwhile the larva is feeding on plancton organisms, as indicated by the frequent moving of its mouth parts. After a while it withdraws its caudal tips from the surface film. It often requires considerable effort for the larva to pull them down into the water. Frequently the larva hangs suspended close underneath the surface, swinging its body back and forth trying to overcome the adhesion between the caudal tips and the surface film. The grown larva is able to relieve itself sooner or later, but to a comparatively young larva this attachment is a constant source of peril. On one occasion the writer found five young larvae, holding one another together with their last prolegs, hanging below the surface helplessly. In failing to swim they all died about a day later. The writer corked an eight-ounce bottle completely filled with salt water in which were a few larvae. A large air bubble was unavoidably left on the under surface of the cork in contact with the water. After five or six hours most of the larvae came up, getting around that large bubble, and remained there until they pupated. At another time several larvae were screened at the bottom of an aquarium, a piece of wire gauze being placed halfway between top and bottom; the larvae thus barred from reaching the surface were suffocated.

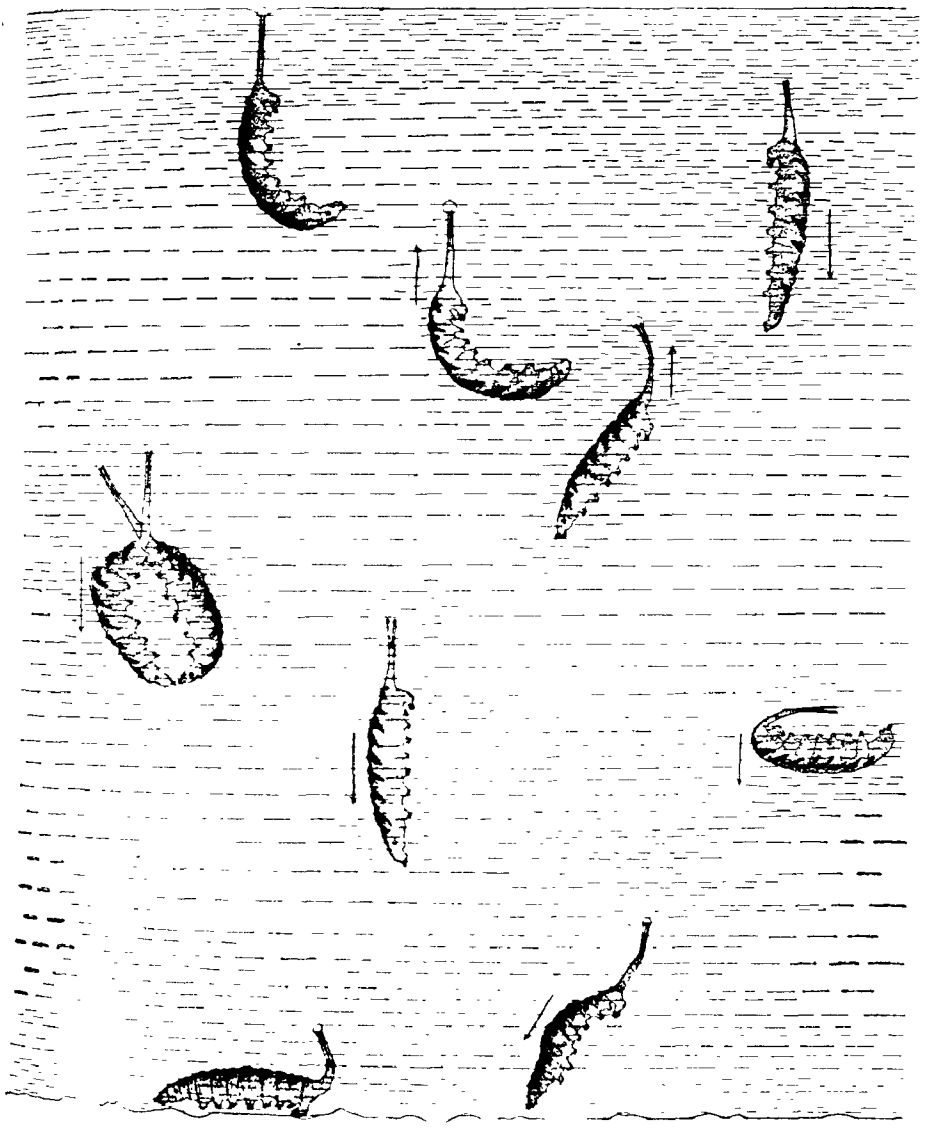

FIG. 73. RESPIRATION ACTIVITY

The writer observed the following interesting phenomenon relative to respiration. The water in the aquarium was thick with microscopic organisms and was greenish in color. Each of the several larvae crawling at the bottom had a bright silvery air globule attached to the caudal end. The size of that globule was as large as the head of the larva. Soon the globule became larger, and the larva floated up with it. As the larva touched the water surface with its caudal end, the silver globule suddenly burst and the larva immediately sank down to the bottom. Sometimes it took about ten or even thirty seconds for the larva to break the globule after it reached the surface. While the larva was in its course toward the surface, it lay straight, curled obliquely, or wriggled and clasped another larva with the last pair of prolegs. But whatever the position or movement the caudal end was always pointing upward. The air globule began to form when the larva was sinking down halfway or sometimes very near the bottom, and its size continued to increase thereafter. After the larva had crawled along at the bottom for about 5 or 6 centimeters, the globule gained its full size and the larva was ready to float up again (fig. 73). This rising and sinking of the larvae kept them restless and gave the aquarium a most lively appearance. It is believed that such action as this takes place only when the conditions in the aquarium are getting abnormal and unfavorable for respiration.

Preference for stagnant and shallow water

The conditions at the pools and overflowed areas are, throughout the season, admirably favorable to the life of the larva. It prefers stagnant water, because it wriggles and suspends itself under the surface, and, because of the absence of specially adapted apparatus, it is unable to gain foothold or to pursue its course in rapid streams. The larva prefers shallow water, because it is easy to reach the surface, where respiration takes place, and because the floating scums offer food supplies. The pools have no outlets, and the water, which is accumulated from rains in the summer season, remains permanently still and has never exceeded 40 centimeters in depth, so that the development of the larval life here is much favored. The presence of larvae in great numbers indicates that these pools serve as an excellent habitat. At different times of the season the salinity and density of the water vary greatly. Some of the pools have a sudden decrease of larvae owing to the over-increase

of these two factors, but the stagnant and shallow conditions, nevertheless, remain ever favorable to their life. The existing conditions at the overflowed areas, likewise, give a good evidence of the larva's preference in such a habitat. The water in these areas, like that in the pools, is always still and never more than 10 centimeters deep, and here are found the larvae in great abundance. Over the surface, thick brown scums for sheltering and feeding make another favorable addition for the inhabitants.

The running water in a narrow creek near this location has not been permanently inhabited by the Ephydra larvae. Once or twice, after several days drought, when the water was reduced to a low mark and became fairly stagnant at its shore, adults began to gather around and a few young appeared, crawling at the muddy bottom. But not long afterward, when a rain brought the water up to its original depth, flies were no longer able to alight on the surface and all the larvae disappeared in the rapid currents. In the pools, the ditches, and the overflowed areas at the salt works in Syracuse, similar conditions exist. At different points where the water runs in a low stream, some larvae were found drifting along without being able to make a stop or to direct themselves to shift to a favorable recess.

Preference for salt water

General range of percentages of salt in water.—Some marine animals placed in fresh water have their blood and body fluid disturbed through osmotic pressure; consequently death may ensue before osmotic equilibrium is established. On the other hand, if the percentage of salt in the water is greater than that in the animal's blood and body fluid, the same result also may follow. So neither hypertonic nor hypotonic solution is suitable for the larvae to live in, but between them there is a general range of percentages of salt that serves as an optimal medium. To this physiological factor is largely due the distinction in adaptation between the salt- and fresh-water animals. The full grown larva of *Ephydra subopaca*, however, does not seem to be materially affected by either salt or fresh water. It is partly due to the circumstance that it has stopped feeding when pupation is imminent, and partly due to the condition of the body wall, which is gradually hardening to a puparium and has become impermeable. Thus the larva has been enabled, to a certain extent, to

stand the unfavorable external medium. In proving this the writer had several grown larvae kept in fresh water, which pupated afterward without difficulty.

Young larvae of the first and second instars, however, require salt water. None of the young larvae placed in a fresh-water aquarium for a period of three days survived, although food was provided. During the growing period the larva requires conditions near to the normal — that is, a range of percentages of salt in water, within which only a little osmosis takes place between the external and the internal medium. In solving the problem of that general range, four sets of experiments were performed.

In Experiment I, the young larvae were able to live in the water having low percentages of salt, while the older ones thrived better in the water of higher salinity. In Experiment II, most of the larvae could live in the salinities ranging from 1 to 8 per cent. Certain chemical substances dissolved in tap water may have had some effect, to a certain extent, upon the larvae, yet the results are plain enough to indicate their adaptability within a fairly wide range of different strengths of salt in water. In Experiment III, those larvae living in water having a salinity of from 1 to 9 per cent attained full growth and pupated, while those in a salinity of 10 per cent died one day afterward. The fact that 10-per-cent salinity is the maximal limit, beyond which no larva could live, is well shown in Experiment IV, even in the case of comparatively mature larvae. It is difficult to rear larvae of the first and second instars in salt water prepared in the laboratory; but in the water collected from the pools it can be done easily, even through all the stages of a complete life cycle. This difference may be due to the foreign food used, such food being less nourishing to the young larvae than the natural. And it is also due — perhaps chiefly — to the enriching nitrogenous substances brought to the pools through animal pollution. Such substances are entirely lacking in the laboratory aquarium. But in spite of these complications, most of the larvae did live and attain maturity within a general range of salinity of from 1 to 9 per cent, as shown in the four experiments.

Garrey (1904) says, "A dilution or concentration of the aquarium water always causes an equivalent in the blood of the invertebrates, and osmotic equilibrium between the 'external and internal media' is established." In the pools the salinity varies from time to time; rain often lowers it

and drought raises it. The adaptability to such wide range in salinity enables the larvae to survive in frequently changed conditions; and the frequent variation of salinity in the season favors the larvae in one way or another during different instars, and, as a whole, gives them plenty of chance to avoid fatalities.

Migration experiment.— The physiological significance of the larva's preference for salt water has been shown in the last paragraph. Such preference can be shown by its behavior equally well. On this an experiment was performed: In a metal plate having two series of compartments, each series was prepared as miniature aquaria by filling with fresh and salt water in alternate order. In each of the aquaria containing fresh water, six larvae were placed A narrow piece of cheesecloth was placed as a bridge between each two adjacent compartments, with each end reaching as far as the center of the bottom of each aquarium. The gentle slope along the cheesecloth immersed in the water afforded the larva a path for climbing over the bridge. Just one day after they had been placed in the aquaria fourteen of the twenty-eight larvae migrated to the salt water. Later the fresh water unavoidably became salty through the capillary action in the cheesecloth, but the rising salinity in the salt water was checked to a certain extent by a little fresh water being dropped in from time to time. Finally two larvae migrated back, while the other twelve remained. These observations are perhaps too few to warrant drawing conclusions, but it may be assumed that osmotic pressure acts externally and internally, and that it is a constant stimulus to the larva when it is subjected to a hypertonic or hypotonic solution The larva is sensitive to such difference from the two media through contact with the external medium by its body wall as well as by its alimentary canal. Moreover, even within such range (1 to 9 per cent) as previously mentioned, in which the larva is able to live, there is still a further preference for percentage of salt as an optimal range for each individual larva, or at least for each instar, as shown by the larva's migrating back to the water with a salinity of 4 per cent from that of 8 per cent.

Factors influencing habits

Absence of air.— The larva is well equipped with particularly developed structures that enable it to stand some of the unfavorable conditions

to which it may be accidentally subjected. For example, the thickened, impermeable body wall of the mature larva, as already discussed, has enabled it to survive and attain pupation in water with a total absence of salt; the convoluted alimentary canal stores enough food for the larva in tiding over a period of starvation, when it happens to face scarcity of food in the water; and, likewise, the larva owes to its complex tracheal system its ability to stay at the bottom for a considerable length of time without obtaining air from the surface, when the conditions there are unfavorable and abnormal. The writer has not been able to observe the effect of total absence of air upon the larva, but inability to withstand deprivation of air has been tested in the following experiments, in each of which a glass relaxing jar 7 centimeters in diameter and 5 centimeters in depth was used as an aquarium.

Experiment I.— Four larvae were placed in water 40 millimeters deep, with a kerosene layer 5 millimeters thick. After twenty hours one larva was dead, and three were alive but moribund, and with air bubbles at the caudal tips.

Experiment II.— Four larvae were placed in water 40 millimeters deep, with a kerosene layer 4 millimeters thick. After twenty-two hours two were dead, and two were alive but moribund.

Experiment III.— Four larvae were placed in water 30 millimeters deep, with a thin kerosene layer. After twenty-four hours the larvae were all alive; after forty-six hours they were still alive but moribund, and some of them had air bubbles at the caudal tips.

Experiment IV.— Four larvae were placed in water 20 millimeters deep with a very thin kerosene film, barely enough to cover over the water surface. After twenty-four hours all the larvae were alive; after forty-six hours one was dead, and three were alive but moribund, and with air bubbles at the caudal tips.

In these experiments the larvae were deprived of a chance to come up to an open surface for respiration, and the air in the water underneath was very much limited in amount on account of the small volume of the aquaria. The great complexity and rich ramification of the tracheal branches must enable the larvae to store enough air to sustain their lives. The length of time through which they lived is directly proportional to the quantity of water from which they could gather dissolved air, and inversely to the thickness of the kerosene layer, which, though never

mixed with water, may contaminate it to a certain extent. The writer observed that when some larvae reached the top layer of the water, with their caudal tips in contact with the floating oil, they seemed to be repelled by it.

In the pools and overflowed areas the water often has greasy films spread here and there upon its surface, but there are enough exposed areas that give the larvae a chance to come up to the surface for respiration. Furthermore, the quantity of water underneath the films is sufficient to keep much oxygen in solution.

Temperature.— Throughout the summer the average temperature of the water in the pools is 25° C. Taking this temperature as a mean, the writer subjected the larvae to various thermal conditions in order to find out how high and how low a temperature they could stand. In an aquarium provided with suitable conditions, two larvae were kept in a temperature of from 27° to 28° C. They lived therein perfectly well. Feeding, wriggling, and crawling, as usual, they did not show any change in habit for fourteen hours. Afterward the observations were interrupted. The temperature was then raised to from 35° to 37° C. and two larvae were introduced into the aquarium, where they were found alive after eleven hours; but after nine more hours they died. When the temperature was raised again, wavering between 38° and 49° C., the larvae wriggled vigorously. Continuing to live for two hours, they were removed to another aquarium, in which the temperature permanently registered 42° C. There the two larvae died within thirty minutes. This experiment was repeated by placing two fresh larvae in a third aquarium in which the temperature varied between 40° and 44° C. These larvae died within one hour. In addition to this it was found that two grown larvae did not live longer than thirty minutes under a temperature of from 43° to 46° C. The writer concludes that a temperature of about 40° C. is the highest limit the larva can stand.

The larva exhibits a remarkable ability for enduring low temperatures. A larva was placed on ice for periods of ten, twenty, and forty minutes, and one hour, and at the end of each period was removed to water of ordinary temperature. However paralyzed the larva was while staying on ice it would soon recover and become lively again after a few seconds. Mature larvae were kept on ice for twelve and twenty-four hours, respectively. Though they seemed dead while on the ice, each was found to

be alive when replaced in water of ordinary temperature. It is safe to assume that the larva can live in water at the freezing point for a still greater length of time, if no other detrimental factors are involved.

Light.— In order to minimize the influence of temperature, the experiment having to do with the effect of light was performed outdoors on a sunny afternoon in the latter part of October. The temperature on that afternoon registered 14° C. Twenty-two larvae were placed in a dish 14 centimeters long and 10 centimeters wide, containing water about 2 centimeters deep. A piece of board covering about two-thirds of the dish was laid over the top to produce a shade. Under bright sunshine the larvae had crawled around in water, but about half an hour after the shade had been placed over the dish, fifteen of the larvae came under the shadow. The board was then removed, and the dish was slightly jarred in order that the larvae might be evenly distributed. When the shade was again replaced, similar results happened within half an hour. This time six larvae were crawling in the light but all the others had gone into the shade. Then the dish was turned around and the formerly shaded part was now exposed to light. At the end of half an hour twelve larvae came quite to the end of the shaded part, two stopped at the middle, while the others were entangled together and with some plant materials in the water, and were moving back and forth at the border between the light and the shade. According to the behavior of the majority there seemed to be a general tendency among the larvae to evade light.

At noontime during midsummer the larvae living in the overflowed areas were found hiding themselves under the floating scums. In the pools they stayed at the bottom or at a considerable distance below the surface. This may have been due to the excessive heat from the direct rays of the sun so that light alone may not have been solely responsible. In the latter part of October, over a great part of the overflowed areas numerous larvae were aggregated along the side where the water was exposed to the morning sunshine, while at the other side, where the delta deposit produced an extensive shadow over the water, very few were found. The larvae were attracted probably by the warmer temperature in the morning, after they had endured a frosty night.

Desiccation.—The larva can stay out of water for a considerable time, provided the soil retains enough moisture. In midsummer, when hot

weather prevails, the water in the overflowed areas is rapidly diminished by evaporation and a great number of larvae are left on land. They sluggishly but steadily crawl about, seeking recesses in the soft mud. They come to some rocks, pebbles, sticks of wood, and the like, that are scattered here and there over the areas, and hide underneath.

Large numbers of larvae stay quite away from the shore, in the deeper water, and retreat with the receding water into deeper parts until finally the water is all gone; then they embed themselves in the soft mud and their dorsa are covered with dirt and scums. Such a covering is a great protection to the life of the larvae in dry weather. Two or three days after the water had receded, a larva was picked up from the mud or from the underside of a log or a rock and placed in water. It was found alive, crawling and wriggling as usual.

In midsummer, showers or gentle rains frequently flood the temporarily dried areas and the bottom mud becomes soft. Both the hidden and the embedded larvae begin to crawl, often producing long trails on the surface of the mud by the scratching of the last pair of prolegs of each larva. These trails are numerous, and are arranged irregularly and often of considerable length. They look like the prints made by pressing a bunch of twisted threads on the mud. In the laboratory some mud brought from the salt pools was entirely drained of water and a number of larvae were placed in it. They behaved just as those had done outdoors — that is, hiding themselves under pebbles and embedding themselves in the mud. Afterward, larvae picked up from the mud and placed in water were always found to be alive. At the end of the fifth day, they were found dead in the thoroughly dried mud. With such ability for resisting desiccation, the larva has much chance to get through a drought that does not last very long. The mud in the overflowed areas is always moistened by dews at night, and as long as moisture is present in the mud the larva will be able to live. Consequently, throughout the season very few larvae have been found killed by drought.

Gravity.— In summer and fall, when the larvae are active in swimming and feeding, they often float up to the surface and stay there for some time. They rise easily, but go to the bottom only with considerable effort. In the laboratory, when a grown larva is transferred from one aquarium to another it seldom goes to the bottom; it is often buoyed up again after it has been forced down.

In an aquarium with several larvae at the bottom, a piece of narrow board was placed at an angle of 60° with its upper end projecting slightly above the water. About an hour later two larvae had climbed to the top of the board, three were halfway up the board, and one was starting to climb. An electric light was then turned on and held about 13 centimeters directly above the water surface. All except one of the larvae started to go to the bottom. Then the light was turned out. At the end of an hour two larvae were climbing again, one of which was very close to the surface of the water. In repeating this experiment several times, whenever no light was hanging there the larvae steadily climbed toward the surface. Sometimes even after the light was turned on, they refused to go down but hid themselves in shade on the lower side of the board or under some floating leaves. The writer has frequently noticed that in the pools under the sun's direct rays the larvae hide themselves under floating boards, scums, and the like, in order to stay nearer the surface.

Mechanical injury.— The larva has been found incapable of regenerating any part lost from its proleg or caudal process. Cutting off the respiratory spiracles interferes with the normal process of respiration. Owing to the amount of air stored in the richly ramified tracheae, the larva is able to live for a short time. In one instance the larva died soon after one of the oral lobes was snipped off.

THE PUPA

Pupation and perching habit

When the larva is ready to pupate, it approaches some object and grasps an edge with its sixth and eighth pairs of prolegs. At this time it ceases its activities in feeding and swimming, the larval skin gradually hardens, and the wrinkles on it disappear. Its color becomes darker and darker, until it is homogeneously brown. The head region, including the first four segments, becomes depressed or slightly concave on the dorsal side and convex on the ventral side. Thus the outline resembles that of a shovel, but it is slightly narrowed toward the anterior end. The pupa perches rigidly on its support (Plate LVII, 43), secure for the transforming period. It is hard to remove it by jerking or shaking. A great number of pupae may be found perching side by side on a stick,

a cord, or any other object, either immersed in, or exposed outside of, the water. All will, however, live through the transformation period. Failing to find any other object of attachment, a larva may grasp the dorsum of another larva's abdomen. Three or four, or even more, may so hold together and drift around in water.

The spiracles in the prothoracic stigmas and at the caudal tips are still functional after pupation has commenced, and continue so until the internal metamorphosis is completed, when the tracheal trunks become atrophied. The air stored within the puparium will be sufficient for the needs of the pupa for the time being. When the pupa matures and more air is needed, the adult will emerge.

The puparium is brownish, with pigmented spots on the dorsum. A well-pronounced edge is formed around the margin of the anterior end. The prothoracic stigmas now stand out laterally. Each is conspicuous with its four digits. The branches of the caudal process diverge laterally instead of pointing straight backward (Plate LVII, 42). When the pupa matures, its body contracts and separates from the wall of the puparium. The pupa is enveloped now in a transparent membrane. The head is broad, with two small antennal tubercles and well-shaped compound eyes. The proboscis is flattened in a truncate piece closely overlapping the coxae of the anterior legs. All three pairs of legs are closely pressed ventro-laterally. The wings are ensheathed by membranes, through which the convolutions of the veins are visible. Closely cephalad to the base of each wing there is a brown, knob-shaped spiracle (Plate LVII, 41).

Length of pupal period

The length of the pupal period varies greatly. The amount of food that the larva has taken before pupation, the location that the pupa seeks, temperature and moisture, rain and sunshine, and the salinity and the density of the water — in other words, both the internal and external conditions — have considerable influence upon the development of the pupa. Pupation records made in the laboratory are as follows:

Beginning of pupation	Emergence of adults	Number of days
June 29	July 10	11
June 30	July 6	6
July 26	August 4	9

Beginning of pupation	Emergence of adults	Number of days
August 2	August 4	2
August 4	August 13	9
August 8	August 13	5

According to the foregoing data, the length of the pupation period varies from two to eleven days. In the field, during hibernation, the period extends over four or five months.

Relation to environment

In different kinds of solutions

A number of pupae were kept at the bottom of a salt-water aquarium. Within ten days many flies emerged. The emergence of about the same number of pupae kept in tap water took place much later. In 5-per-cent formalin, adults emerged from the puparia floating on the surface, but in kerosene all the puparia sank to the bottom and none of the pupae developed.

When exposed to air

From the salt pools a stick of wood with numerous pupae attached was brought into the laboratory. Before the laboratory was reached, a few flies emerged. More continued to emerge in the laboratory before this piece of wood became entirely dry.

Effect of excessive heat

High temperature, within a certain limit, favors the development of the pupa and hastens the emergence of the adult. During the latter part of July the temperature in the laboratory registered about 30° C. The pupae kept in the laboratory did not show any unusual speed in development. After several days of sunny weather, the temperature rose steadily, registering between 39° and 40° C. at noon. Under each of three bell jars, from twenty-two to twenty-four half- or full-grown pupae were placed. At the end of the first day, from three to five adults had emerged in each jar; two days later the number had increased to six or eight; and at the end of the sixth day, to fifteen or twenty. This is assumed as the highest temperature the pupae could stand in the presence of plenty of moisture. In order that this assumption might be verified, the same

number of pupae were kept in bell jars in a greenhouse where the temperature registered 45° C. between 1 and 2 p. m. In this experiment all the pupae died at the end of the day.

THE ADULT

Emergence

The transformation to the adult stage was observed in the laboratory. The fly came out by breaking off the oval disk of the dorsum at the anterior part of the puparium. It struggled at the opening of the pupal case, but finally emerged without much difficulty. Each of its legs wrinkled like a French curve, and its ptilinum bulged like a glass globe. The ptilinum, with its somewhat pubescent surface, expanded and contracted at short intervals for about thirty minutes. The ptilinum then sank into the head, leaving a transverse cavity in the front. The sinking was gradual, and the ptilinum was pushed out again several times, but each time the pushing was weaker. Finally the cavity at the front was gradually narrowed to a very thin cleft. The fly moved around on the water surface and frequently rubbed its abdomen with its hind legs. About a quarter of an hour later it began to rub the tips of its wings. Through constant rubbings the wings began to expand at their tips, until they became straightened and entirely spread. The fly then gave a few more strokes and was ready for flight.

Food and feeding habits

The alimentary canals of ten flies were dissected and examined. The contents consisted almost entirely of Chlamydomona and Navicula. Bacteria, Mastigophora, and inorganic materials were found only occasionally.

Ephydra subopaca feeds in the same manner as does the house fly, but resting on water, on the floating scums, on leaves and the like, in the pools or on the surface of soft mud.

Preference for stagnant water

A calm water surface is most favorable for flies. They do not fly any considerable distance, and never higher than a foot above the surface;

neither do they hover over the water surface and dance in the air. Rapid streams are unfavorable to them, and they shun even slow-running currents. Because of the ripples at the shore, not a single fly was found in the lake, regardless of the proximity of the pools and overflowed areas.

Factors affecting the adult

Absence of salt in water

Unlike the larva, the adult does not require salt; it lives on the surface of salt water, but it lives on fresh water also. In the laboratory, adults were often confined on the surface of fresh water immediately following their emergence. Food was provided, and the flies lived, in most cases, from six to twelve days.

Heat

A newly emerged adult subjected to a temperature of 36° C. in the greenhouse died within three hours. A second one, kept in the same confinement but at a temperature between 25° and 26° C., lived until the next afternoon, when the temperature suddenly rose to 34°. The conditions here were, however, different from those outdoors. There was no shade for the fly to seek and no current of air, and the fly itself was deprived of liberty in changing from one place to another. Therefore in the field a temperature of 35° might not have affected it fatally.

Rainfall

Excess rainfall is beneficial to the adults in that it widens the water surface of the overflowed areas, maintains the normal salinity in the pools, and eliminates the chance for the loss of the natural habitat.

From the data gathered during the months of June, July, and August, in the two years 1916 and 1917, it was seen that the number of flies materially increased during the periods of greater rainfall.

Frost and snow

Unless frost is extremely heavy, it has very little effect on the adult flies. In September, when the frost was light there was not much change in the number of flies in the field; but later, when conditions were different, the following records were obtained:

November 1. Considerable frost; no dead flies found.

November 2. Considerable frost; flies very scarce in the pools, but numerous in the overflowed areas.

November 5. Very heavy frost and thin ice; flies on ice hardly able to move when turned over.

November 7. Heavy frost, and warm, bright sunshine; flies lively, staying on ice; six newly emerged flies and three mature flies died.

November 22. Frost and snow; two mature adults found; one newly emerged fly died.

November 28. Snow; no flies found.

Mating

Mating was observed on June 30. The male frequently jumped upon the female, trying to mate, but such attempts often resulted in failure, the female being unresponsive. He clasped the front of the female's head from behind with his front legs, while the middle legs held onto her mesothorax and his hind legs onto the posterior third of her abdomen. By holding her fast with the two anterior pairs of legs, his hind legs were then able to move freely, rubbing on the female's genitalia continuously for about thirty seconds. The female then turned the tip of her abdomen upward. The male's abdomen was held in its usual position while a slender and pointed penis was protruded downward and inserted into the genital opening of the female. Copulation thus took place and lasted about four or five minutes. Then the penis of the male was drawn out, exposed for a while, and was finally withdrawn into his abdomen. He remained on the female for a few minutes before jumping away, but at times the male has been noted to hold the female under his feet for more than an hour.

THE EGG

Oviposition

Oviposition seems to be a very brief procedure. The writer observed a single female oviposit seven times within twenty minutes. Each time a single egg was laid on the water surface by the female's merely touching the latter with her ovipositor. The eggs thus laid immediately sank to the bottom.

Description

The egg is elongated oval in shape and measures 0.9 millimeter in length. Both ends are practically equal in breadth and the egg is slightly

curved at the middle. The anterior end has a micropyle (Plate LVII, 44). The chorion is grayish white, but sometimes slightly pink. The surface is reticulated with hexagonal markings.

Hatching

The egg can hatch in salt water, in lake water, or in tap water. Temperature has marked influence on the development of the egg, for under a temperature of between 18° and 20° C., hatching did not take place until the end of the third day, while under a temperature of 33°, eggs began to hatch after seventeen hours but most of them were killed soon afterward.

As the embryo develops, the mouth and the claws of the prolegs are more or less visible through the chorion. The body is bent in the egg shell. The movement of the claws gives an appearence of wave motions. The mouth parts frequently gnaw on the inside of the chorion, producing a wedge-shaped transparent part. The head breaks the chorion and the opening is enlarged by the forcing-out of the thorax. While the body is wriggling outside, the claws of the last pair of prolegs often hold onto the broken edge of the shell. The larva must struggle before being freed. The emergence usually takes from thirty to forty seconds.

PROTECTION

Ephydra subopaca has several interesting characteristics that serve for protection throughout all the stages in the life cycle. First, it has protective coloration. The egg is grayish opaque and can scarcely be seen when at the bottom of the water; it is sometimes slightly pinkish and is thus more easily confused with decayed plant materials in the salt pools. While crawling in shallow pools, the larva gathers dirt all over its body, making it resemble the color of the muddy bottom and also that of the floating scums. When the larva is mature and ready to pupate, its hypodermis becomes hardened and gradually turns brown, resembling the color of the plant matter on which the pupa perches. The coloration of the adult, as has been described, harmonizes also with its background. Boards, logs, scums, or the surface of soft mud in the temporarily dried areas, with a number of flies scattered here and there, look concolorous—that is, uniformly dull brown; thus a swarm of flies can hardly be distinguished from a distance without careful inspection.

Secondly, the structure is a protective feature. The thick chorion of the egg, the thick hypodermis of the larva, and especially the hard skin of the pupa, enable the species to survive in a wide range of salinity and under various unfavorable conditions, and protect the insects from being harmed by mechanical means.

Thirdly, the habitat seems to be protective in character. As already mentioned, eggs laid on the water surface sink to the bottom, and thus are avoided certain catastrophes that might be caused by temperature, climate, or mechanical agents. Furthermore, eggs are laid singly. Being so minute in size, they are by no means easy to detect by any predacious insect in the pools. The larva has a hiding or shelter-seeking habit. The perching habit of the mature larva has made the animal most inconspicuous in its environment, and this is true also with the adult's habit of resting on water surface or on mud where the scums afford a harmonizing background.

Fourthly, the adaptability of the species to such a unique habitat is in itself protective. The salinity and density of the water unfit these pools as a habitat for most of the aquatic insects that thrive in fresh water. This keeps this species from contact with certain predacious forms.

ENEMIES

Since this species is so well protected, it is largely free from attacks by insects. In early morning, the writer has often seen flocks of sparrows feeding on the ground near the pools, but never did they attempt to feed on the larvae which were so numerous in the mud and shallow water. Herring gulls and kingfishers were seen several times flying over this region from the lake, and the latter often stopped somewhere near the pools, but never has the writer been able to see them feeding on the immature stages of the fly. Domestic fowls, on the other hand, are enemies of this species. Throughout the season fowls' footprints were often found on the mud in the overflowed areas, and several times the fowls while hunting for food were seen to pick up larvae or pupae. Among insects, the only enemy observed was one of the common water striders, *Gerris marginatus*. Once a fly was noticed turned upside down on the water surface, before it regained its natural position it was caught by a water strider. The strider carried the fly around on the surface for about a quarter of an hour, but finally it disappeared in the grasses along the shore.

Not long afterward it came out again with the prey still in its possession. There may be more enemies among the insects, but no others were observed. The writer once found a water mite, Limnochares, attached to the cheek of an adult fly, as an external parasite.

DISPERSAL

Ephydra subopaca may be dispersed, perhaps for a long distance, during the pupal stage. As already mentioned, it is impossible for the adult to make a long journey on the wing. Since the larva, although able to crawl in soft mud, has no means of locomotion elsewhere after the moisture in the mud is all gone, there is no chance for it to travel from one place to another. As soon as the prepupal period is at hand, the perching habit enables the animal to secure stable foothold. Then there comes the possibility of migration, because wherever the supporting object is shifted, the pupa will go with it. Dispersal is facilitated by three characteristics of the pupal stage — one held in common by all insects, and two particularly pertaining to this species: first, during the pupal stage, the animal does not require food; second, the pupa always has a very firm hold on its support, so that there is no danger of its being shaken off; third, the thick and hard puparium enables the animal to stay outside of water for some time, and also serves, as already mentioned, for protection from injury during its journey.

Many times the writer, in lifting a fragment of wood from the pools, found hundreds of pupae, both mature and young, scattered along the edges of the stick. These could never be removed by shaking or jerking. Several times an enormous number of pupae were found firmly attached to a piece of cord which had been thrown into a shallow pool. Whether in water or in the soft mud area, or exposed to the air, these pupae are able to attain maturity if no extremely unfavorable conditions occur. Attached to such supports, they may be brought from one place to another by train or other carrier, and thus dispersal of the pupae may be accomplished.

Aldrich (1912) lists the localities where this species has been found as follows: Massachusetts, Woods Hole (Melander); Connecticut (Loew); New York, Ithaca, at salt pools (Johannsen); New Jersey, several localities (Smith catalog); Illinois, Gallatin County, at salt pools (Packard); Utah, Box Elder Lake, in salt water, Garfield in brackish seepage, Promontary Point in brackish spring; Idaho, Market Lake, in overflow from

irrigating ditch; Nevada, Hazen, in overflow from irrigating ditch; Winnemucca Lake, in alkaline environment; Walker Lake, in alkaline environment; California, Mono Lake, in near-by seepage; Washington, Soap Lake, Grand Coulee, in alkaline environment.

Aldrich states that the density of the water (salt or alkaline) in which this particular species lives is subject to great fluctuations.

From the experiments described herein, proving that larvae of *Ephydra subopaca* can live in salt solutions of different strengths, varying from 1 to 9 per cent, it follows that there is an ample chance for this species to survive in pools or lakes the salinity of which falls within such limits.

SEASONAL APPEARANCE AND METEOROLOGIC CONDITIONS

To temperature and humidity is largely due the seasonal appearance of this species. Warm weather in late spring causes the adults to appear early, and high humidity in summer causes all stages to appear in great numbers throughout the season. The weather records of the two seasons 1916 and 1917 are different in this respect. In the year 1916 the species appeared much earlier than in the year following, while in 1917 there was a greater abundance of both the adult and the immature stages than in the year before. These differences were due mainly to the temperature and the rainfall in the spring and summer of the two years.

According to the report of the United States Weather Bureau at Ithaca, New York, the average temperature for May, 1916, was 57.6° F., while that for 1917 was 48.4°. The work of the writer began in June, 1916. Although the first appearance in the preceding month was unfortunately lacking in the field record, the field observations convinced the writer that they must have appeared three or four weeks before the work started. During June, adults were found in the salt pools and even in the one the water of which had almost lost its briny character; and the mass of the flies that every day assembled over the water surface did not seem to indicate that they were the ones that appeared first in the season. The writer was informed by Dr. O. A. Johannsen that he had caught many adults in May. The first appearance of the adults is usually in the latter part of this month. In 1917, on the other hand, the appearance was evidently delayed on account of low temperature. Beginning on May 1, the writer frequently visited the pools, looking for adults, but none were found until June 21, when they appeared in large numbers. In June,

1916, larvae and pupae were found in almost every pool, because the adults started to breed early, while in 1917, in the first twenty days, only one or two were found. For such contrast the difference in temperature is considered the most probable cause.

As far as the number in all stages is concerned, the summer of 1917 outstripped the preceding year, in spite of the delay in appearance of the adults. After the adults had appeared, they soon started to breed. High humidity facilitated the hatching of the eggs and the development of the larval and pupal stages, thus bringing forth great numbers of adults. The immature stages were produced in corresponding abundance. There is every reason to believe that the great number of this species found in the summer of 1917 was due to the frequent rains that were so characteristic of that season in this locality. During the previous year the amount of rainfall was considerably less, and this species was correspondingly more scarce.

COMMUNAL LIFE

Being able to live in great fluctuation of density and salinity, *Ephydra subopaca* has a decided advantage over other insects in the salt pools. Here competition or the struggle for existence between this species and all others is by no means keen. Besides *Ephydra subopaca*, the permanent members of the same community consist of five insects, four of which are coinhabitants, while the other is more or less an intruder and an enemy to the adult flies of the species. This latter is the common water strider, *Gerris marginatus*, mentioned in the preceding pages. This insect is, however, very rare. Among the other four the most abundant and common form is the larva of a mosquito, *Aedes currei* Coq. This larva is numerous in some pools and sometimes it outnumbers the species of Ephydra, but it is not able to endure high salinity. Consequently, the larvae have never been found in pools D, E, I, and H, the salinity and density of which are high (page 365).

Rat-tailed maggots are found in most of the pools. They are able to endure a salinity as high as that of pool D, and in this respect they can compete with the larvae of Ephydra; but the number is far inferior, and only now and then one or two are found, so there never could be very much competition for food and shelter between the two species. A few larvae of Culicoides and a great number of Chironomus are also found

in the water of comparatively low salinity, and the writer has occasionally found a few water mites in such water. But with an overwhelming number and an elastic adaptability to various conditions in pools, Ephydra has so far outstripped its coinhabitants in competition that the principal place in this kind of habitat must be assigned to this species.

HIBERNATION

The larvae which do not pupate in late autumn live through the winter. They usually stay at the bottom of the pools and very seldom are found suspended between the surface and the bottom, as in summer. They are motionless and are covered with mud through the accumulation of sediment. It is hard to distinguish them by looking over the surface of the pools; but in the overflowed areas, where the water is hardly more than three inches deep, a large number of them may be found lying on the muddy bottom. Sometimes, when the heat of bright winter sunshine raises the temperature, a few larvae may be seen crawling slowly. They will not pupate in cold weather but will wait until spring.

The pupae of late autumn will remain undeveloped through the winter. Late in the season large numbers of pupae may be found. In the early spring of the next year pupae are always found before any other stage appears. From these emerge the first adults of the coming season.

Adults are rarely found in winter. On a warm and sunshiny morning one or two may appear, feebly drifting around on water. It is believed that they hide themselves in crevices in the gravelly bank and in the loose soil around the pools in order to winter over.

Hibernation in the egg stage, if it occurs at all, must be very exceptional. According to observations made in the laboratory, the females do not oviposit late in the season, even though the room temperature may be comparatively high. Eggs laid in the early fall remained undeveloped for a long period, and some of them died before winter commenced. Thus there is evidently very little chance for them to hibernate in this stage.

SUMMARY

1. *Ephydra subopaca* has a salt habitat. It is found in the salt pools at Ithaca, the density of which ranges from 1.5 to 7+ in August and from 1.5 to 11 in September, and the salinity of which varies from 1.76 to

9.7 per cent in August. The salt pools contain several algae and several protozoa, together with some animal pollution.

2. The growth of the larva is largely influenced by temperature and the presence of salt in water.

3. The larva moves by crawling, wriggling, floating, and dropping. Its respiration is at the surface. Its food consists of algae with few protozoa. It prefers to live in stagnant and shallow water, with the amount of salt ranging between 1 and 8 per cent and a solution of from 4- to 5- per-cent salt in the optimum.

4. The larva can live in a limited area of air. It can endure the variation of temperature from 0° to 40° C. It can survive drought for five days.

5. It is significant with the larva that its specific gravity is less than unity.

6. Any mechanical injury which breaks the hypodermis proves fatal to the larva.

7. Pupation is characterized by the perching habit. The pupal period lasts from two to eleven days in the laboratory and from four to five months in the field. High temperature in addition to desiccation is very detrimental.

8. The food of the adult is the same as that of the larva. The adult prefers to stay on the surface of still water. Excessive heat is very detrimental, but excessive rainfall is beneficial. Only heavy frost has a killing effect upon the newly emerged adult. The adults disappear entirely in winter when snow covers the ground.

9. The egg is elongated oval with a reticulated surface. Hatching takes place in fresh water as well as in salt water. The development of the egg is affected by temperature.

10. The habit, the adaptation, the coloration, and the body structure of all stages are protective. Domestic fowls and water striders were the only enemies observed.

11. The dispersal of this species takes place during the pupal stage and is probably achieved by artificial transportation.

12. The flies appear in May or June. High temperature and high humidity in late spring make for an early appearance. Frequent rains favor abundance of them throughout the summer and autumn seasons.

13. This species winters usually in the larval and pupal stages, although a few adults may live through the winter in hibernation.

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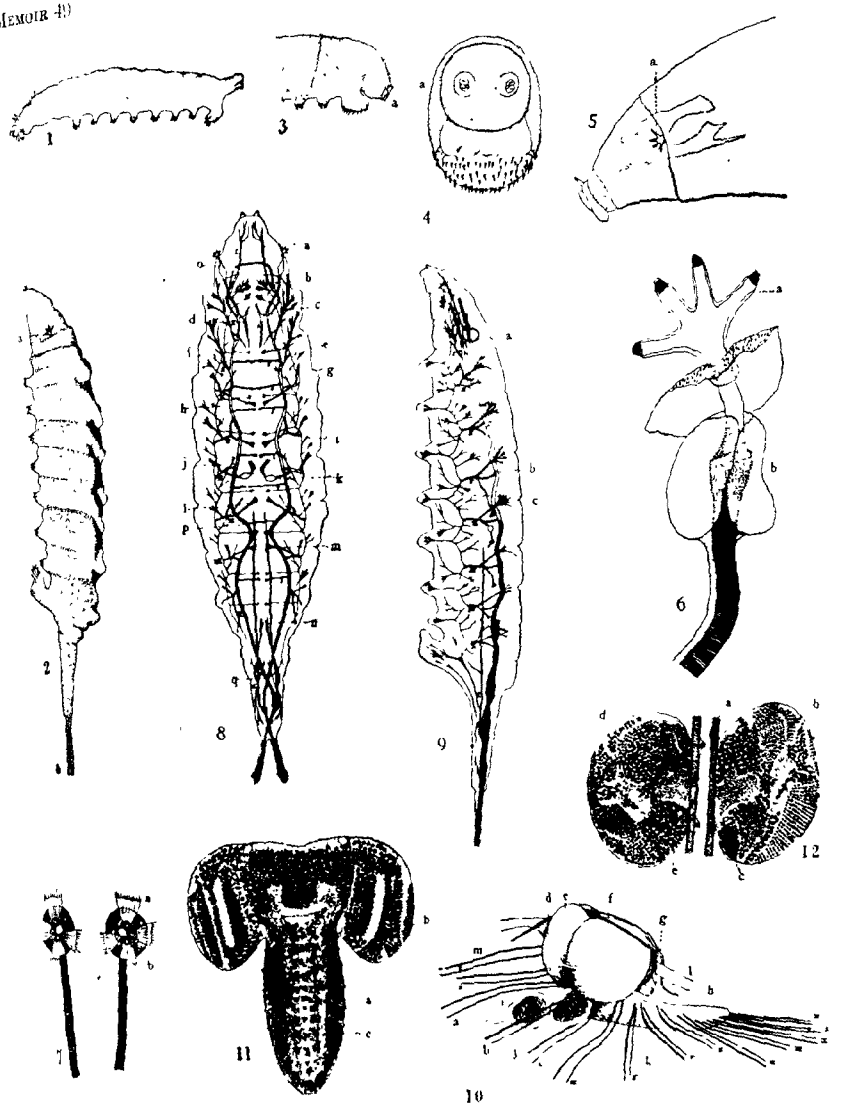
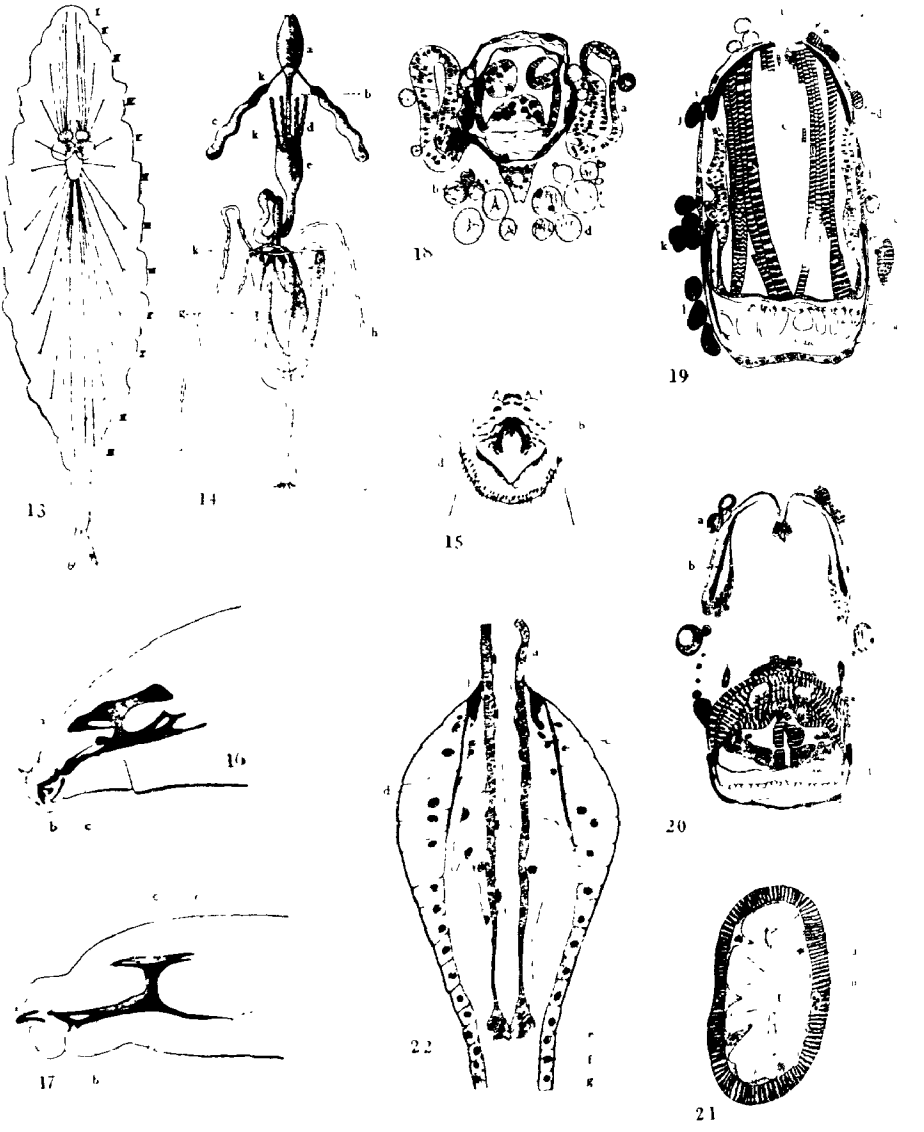


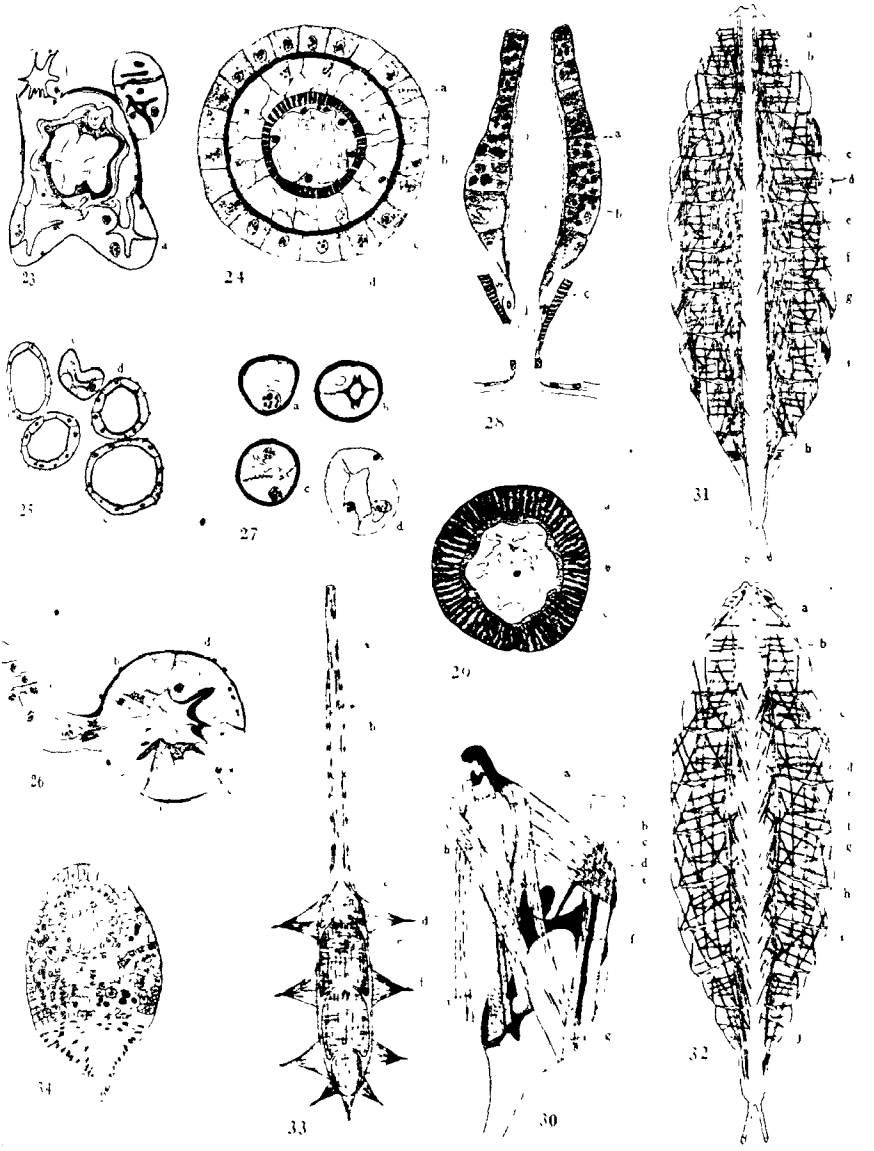
EPHYDRA SUBOPACA

1, First-instar larva; 2, full-grown larva (a, prothoracic stigma, b, posterior spiracle); 3, lateral view of caudal part of first-instar larva; 4, caudal view of same (a, posterior spiracle); 5, relative positions of prothoracic stigma and cephalopharyngeal skeleton (a, prothoracic stigma), 6, enlarged view of stigma (a, stigma, b, muscles of disk); 7, posterior spiracles (a, chitinous membrane, b, spiracle); 8, dorsal view of tracheal system (I-X, outer branches; 1-8, inner branches; a, tracheal branch to muscles of cephalopharyngeal skeleton; b, to imaginal disk; c, tracheal branch to imaginal disk; d, to ring; e, to salivary gland; f, to imaginal disk; g, to dorsal body wall; h, to proventriculus; i, to lateral body wall; j, to mid-intestine, k, to tracheal body; l, to hind-intestine; m, to mid-intestine; n, to hind intestine; o, p, q, commissures), 9, lateral view (a, commissure; b, dorsal trunk; c, ventral trunk); 10, lateral view of nervous ganglion of larva (I-X; segmental nerves; a, b, c, nerves arising from bases of stalks of prothoracic and ventral mesothoracic imaginal disk; d, optic imaginal disk; e, optic stalk; f, cerebral lobe, g, ring, h, subesophageal ganglion; i, prothoracic; j, ventral mesothoracic disk; k, esophagus; l, dorsal aorta; m, trachea), 11, horizontal section of cerebral lobes (a, esophagus; b, retina; c, stroma); 12, horizontal section of cerebral lobes



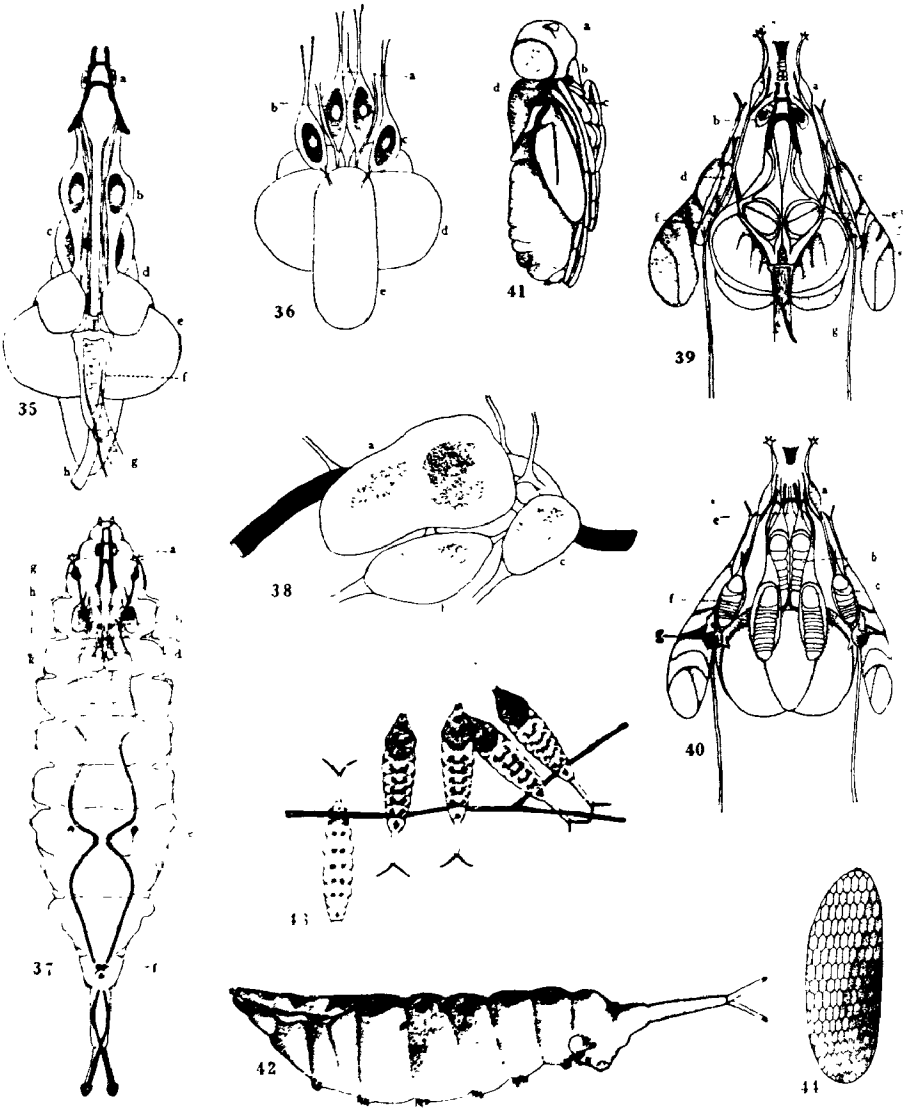
EPHYDRA SUBOPACA

13. Dorsal view of distribution of segmental nerves (I-XII, segments); 14, alimentary system; a, pharynx; b, esophagus; c, salivary gland; d, caeca; e, proventriculus; f, mid-intestine; g, hind intestine; h, malpighian tube; i, rectum; k, imaginal disks); 15, ventral view of oral cavity and second segment (a, antenna; b, mandibular sclerite; c, tubercles; d, hypostomal sclerite); 16, lateral view of region of grown larva, showing cephalopharyngeal skeleton (a, mandibular sclerite; b, dental sclerite; c, hypostomal sclerite); 17, lateral view of young larva (a, mandibular sclerite, b, hypostomal sclerite, c, dental sclerite, d, lateral pharyngeal sclerite; e, pharyngeal mass), 18, cross section of anterior region (a, imaginal disk, b, common duct of salivary glands, c, cephalic retractor muscle; d, ventral muscle); 19, middle pharyngeal region (a, accommodating membrane; d, dorsal longitudinal cephalic retractor, d, pharyngeal sclerite, e, pharyngeal sinus, f, imaginal disk, g, pharynx Y-shaped ridges; i, pharyngeal depressor; j, dorsal cephalic protractor; k, stomal dilator depressor); 20, caudal pharyngeal region (a, cephalic retractor; b, lateral pharyngeal sclerite; disk; d, stomal dilator; e, semicircular dorsal pharyngeal muscle; f, pharyngeal cavity), 21, esophagus (a, circular muscle; b, lumen, c, epithelium); 22, longitudinal section of esophagus; b, imaginal cells, c, blood space; d, sphincter; e, epithelium, or ventriculus, f, branes g, lumen of ventriculus)



EPHYDRA SUBOPACA

23, Cross section, showing insertion of caeca (a, caecal tube), 24, cross section of proventriculus (a, striated border, b, ... c, blood space; d, circular muscle of sphincter); 25, cross section through convoluted alimentary ... b, c, d, mid-intestine; e, hind intestine); 26, cross section, showing insertion of malpighian tub... circular muscle; b, longitudinal muscle; c, epithelium; d, basement membrane; f, malpighian tubes; 27, cross section of malpighian tubes (a, b, c, tubes; d, common root of two tubes); 28, longitudinal section ... rectum (a, epithelum; b, muscular wall; c, muscle); 29, cross section of rectum (a, circular muscle, b, ... c, hutima); 30, muscles of cephalopharyngeal sclerites (a, mandibular extensor, b, pharyngeal ... c, dorsal cephalic protractor; d, e, f, stomal dilators; g, ventral cephalic protractor; h, mandibular ... sor; i, ventral cephalic retractor); 31, muscles of dorsal body wall (a, dorsal cephalic retractor, b, ... annular; c, lateral intersegmental; d, external dorsolateral oblique; e, internal dorsolateral oblique ... lateral longitudinal; g, dorsal longitudinal; h, anal; i, lateral); 32, ventral body wall, with muscles ... cephalic retractor; b, ventral cephalic retractor; c, internal ventral oblique; d, external ventral oblique ... lateral longitudinal; f, intersegmental; g, internal ventro-lateral oblique; h, external ventro-lateral ... i, ventral longitudinal; j, anal); 33, dorsal view of vascular system (a, dorsal aorta, b, ... body; c, valve; d, alar muscle; e, f, ostia); 34, longitudinal section of gonad



EPHYDRA SUBOPACA.

35. Dorsal view of imaginal disks (a, proboscis, b, antennal and frontal; c, prothoracic leg; d, mesothoracic leg; e, cerebral lobe; f, ring; g, dorsal aorta; h, esophagus); 36, ventral view (a, median string; b, prothoracic leg; c, mesothoracic leg; d, cerebral lobe; e, subesophageal ganglion); 37, general arrangement of imaginal disks (a, proboscis; b, antennal and pronotal; c, prothoracic leg; d, optic; g, dorsal prothoracic; h, wing; i, metathoracic; j, haltere; k, mesothoracic; f, anal; e, gonad); 38, external view of posterior thoracic imaginal left side (a, wing; b, metathoracic; c, haltere); 39, dorsal view of imaginal disks of prepupal stage (a, dorsal prothoracic; b, proboscis; c, wings; d, metathoracic; e, frontal; f, haltere; g, optic); 40, ventral view (a, dorsal prothoracic; b, prothoracic leg; c, mesothoracic leg; e, median string; f, metathoracic; haltere; 41, pupa (a, antenna; b, labral part of proboscis; c, coxa of leg; d, spiracle); 42, pupae; 43, pupae perching on stick; 44, egg

MEMOIR 50

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

RELATIVE GROWTH-PROMOTING VALUE OF THE PROTEIN OF COCONUT OIL MEAL, AND OF COMBINATIONS OF IT WITH PROTEIN FROM VARIOUS OTHER FEEDING STUFFS

L. A. MAYNARD AND F. M. FRONDA

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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THE RELATIVE GROWTH-PROMOTING VALUE OF THE PROTEIN OF COCONUT OIL MEAL, AND OF COMBINATIONS OF IT WITH PROTEIN FROM VARIOUS OTHER FEEDING STUFFS

L. A. Maynard and F. M. Fronda

The recently acquired knowledge as to differences in the quality of proteins has reopened the entire question as to protein requirement, and a review of this problem is especially needed with respect to farm animals. It is now evident that the amount of protein required for growth or other function in a given animal cannot be definitely fixed except as the source of the protein is specified. Knowledge is required as to how feeding stuffs should be combined to secure protein mixture of high quality, and a review of the general question of protein requirement is desirable on this basis. It is believed that much valuable information relative to this problem can be acquired by studies with small animals, that such studies will prove a useful guide in planning similar experiments with large animals, and that many of the latter experiments, always laborious and time-consuming, will be made unnecessary by reason of the studies with small animals. The latter studies can most profitably deal with the relative efficiency of various protein sources and combinations, in order to obtain data for formulating rations of high quality, rather than with determinations of the minimum protein requirement for a given mixture, inasmuch as the latter data must be obtained by trial with the large animal in question.

The experiments described herein comprise a study of the relative growth-promoting value of coconut oil meal and of various combinations of other feeding stuffs with it. Coconut oil meal is a high-protein feed which is becoming available in increasingly large quantities and which gives promise of being a valuable ingredient of rations for farm animals, especially dairy cows. There are, however, few data available, either from experimental work or from practice, as to how it should be combined in the ration. A study of the value of its protein and how it can be supplemented to secure a mixture of high quality is therefore timely.

Johns, Finks, and Paul (1919)[1] report a study of coconut oil meal with small animals, from which it is concluded that this feeding stuff contains all the amino acids necessary for growth. Their study, however, which dealt also with vitamine and mineral supplements, was concerned primarily with the question of the ability of coconut-oil-meal protein to cause normal growth, not with the efficiency of the protein as measured in gain per gram of protein eaten — which is the criterion used in the studies here described.

METHOD

In these experiments the method consisted of using the feeding stuff or combination to be tested as the sole source of protein in a diet made otherwise adequate by supplying minerals, vitamines, and an added source of energy where needed. The percentage of protein was so chosen as to make the absolute amount of protein eaten insufficient for normal growth, even though the ration was fed *ad libitum*. Thus, given the same percentage of protein in the various rations, which constituted diets otherwise adequate, a study of the relative growth-promoting value of the various protein sources was possible. White rats were the experimental animals.

The rations were fed *ad libitum*, growth curves and the gain in body weight per gram of protein eaten being used as the measure of growth-promoting value. Although there would have been an obvious advantage in an equal food intake, in which case growth curves alone would have sufficed for judging the efficiency of the different sources, this would have necessitated regulating the food given according to the consumption of the rats that ate the least, and thus, by restricting the intake for the other groups, protein might have been used as a source of energy, which would have defeated the purpose of the experiment. Inasmuch as food intake varied on the different rations, due to differences in palatability and in the individual's appetite, growth curves are not the best measure of the comparative value of the protein sources. Therefore an accurate record of food intake was kept, and comparison is made on the basis of the gain per gram of protein eaten. Growth curves, however, are presented because of their value for comparing a given growth with the normal, and for judging the uniformity and regularity of gains of individuals fed alike.

[1] Dates in parenthesis refer to *Literature Cited*, page 633.

The feed was kept before the rats constantly, a fresh supply being given every other day. It was packed into the feed dishes with sufficient water to prevent its being scattered about the cage, in order that any not consumed could be recovered and accounted for. The unconsumed feed was deducted from the amount fed, after making a proper correction for the water added. This correction was made possible by running moisture determinations. The rats were weighed weekly.

EXPERIMENTAL

Series I

The first studies consisted of a comparison of the growth-promoting value of coconut-oil-meal protein and cornmeal protein, singly and in combination. Cornmeal was selected because it is a widely used feeding stuff, containing proteins the quality of which has been fairly definitely established. With the choice of this feed, the choice of a plane of protein intake was limited by the percentage of protein that a ration consisting of cornmeal, properly supplemented by the addition of a salt mixture and a vitamine, would furnish. The work of McCollum, Simmonds, and Pitz (1916-17) furnished a guide here, in that they found that all factors for the growth of rats, except protein, were adequate in a ration consisting of

Cornmeal	91
Salt mixture	4
Butterfat	5

and that the protein furnished (approximately 9 per cent) allowed growth to proceed at two-thirds the normal rate. The plane of protein intake thus furnished, giving a fairly rapid yet not normal rate of growth, was deemed satisfactory for the present purpose, and the ration used by McCollum and his coworkers was chosen as the cornmeal ration in these trials. The salt mixture employed was the one described by the latter investigators in the publication cited.

The analysis of the cornmeal used in these experiments fixed the protein content of this ration at 8.93 per cent. Next, a ration containing coconut oil meal as the sole source of protein was made up with the addition of

the necessary amount of starch to hold the protein at the same figure as the cornmeal ration, as follows:

Coconut oil meal	43
Cornstarch	48
Butter	5
Salt mixture	4

The protein content of this ration was 8.99 per cent. That such a ration is adequate for normal growth except for its protein content is indicated from the study of Johns, Finks, and Paul (1919), who found that coconut oil meal contained adequate water-soluble vitamine, and that when this feed was supplemented with a salt mixture and fat-soluble vitamine, practically normal growth resulted.

A ration was next made up in which 25 per cent of the corn protein was replaced by coconut-oil-meal protein. Sufficient starch was added to keep the protein content the same as in the cornmeal ration, the percentage of butter and the salt mixture remaining the same.

Inasmuch as an efficient protein mixture was the object sought in these experiments, the question arose as to what growth-promoting value could be expected from an ideal mixture at the plane of intake used, namely, 9 per cent. In view of the high quality resulting from a mixture of cornmeal protein and skimmilk protein, it seemed worth while to obtain data on this combination at the plane of intake used, in order to establish a standard with which the results with the other combinations could be compared. Accordingly, a ration was made up in which 25 per cent of the cornmeal protein was replaced by skimmilk protein, the butter and the salt mixture remaining the same. Starch was again used to keep the proper percentage of protein.

Three rats were placed on each of the above-described rations. The experimental period was thirteen weeks.

The growth curves for the trials in this series are shown in figure 74. A summarized record of food intakes and gains is given in table 4. Inasmuch as more or less trouble was experienced during the first week in accustoming the animals to the ration, resulting in a wide variation in the food intake, this period was set apart as a transition period, and the records for the remaining twelve weeks were summarized into three periods of four weeks each. The figures for the transition period are not included

in the figures for totals and averages. The figures for gains classified as "Totals" are the means of the individual gains over the twelve-weeks period. The probable errors of these means were computed by Peter's formula.

Series II

A measure of the efficiency of the protein of coconut oil meal as compared to that of corn having been obtained in series I, and the supplementary action of the two sources having been studied, attention was next directed to combinations of coconut oil meal with representative feeding stuffs from various plants. Inasmuch as coconut oil meal is a high-protein concentrate, low-protein feeds were selected as supplements. Those used were wheat middlings, rice bran, ground kaffir corn, alfalfa leaf meal, and alfalfa meal. Rice bran and kaffir corn are feeds from plants commonly grown in regions where the coconut palm is extensively cultivated. The alfalfa products were chosen in order to gain some idea as to the value of a combination of coconut oil meal with a leafy roughage. First, alfalfa leaf meal was tried, but for some reason the ration containing it was not palatable and so much less of it was eaten in the first few weeks than of the other rations that another trial was started using alfalfa meal instead.

Substitutions were made in the coconut-oil-meal ration given on page 624 so as to have the supplements furnish 25 per cent of the protein. The starch content was varied as was necessary to maintain the protein constant at 9 per cent. The salt mixture used was the one described by Osborne and Mendel (1919). The combination that proved the most successful, namely, rice bran and coconut oil meal, was repeated at a plane of intake of 15 per cent protein. Three rats were fed on each combination and the experimental period was the same as in series I.

The curves of growth are shown in figures 75, 76, and 77. The gains in relation to food intake are shown in table 2. Probable errors for the mean total gains were computed as described under series I.

DISCUSSION OF RESULTS

It is shown in figure 74 that the cornmeal and skimmilk mixture caused a rate of growth very close to normal, but that the other rations were much less effective. The cornmeal alone produced the slowest growth. In table 1 it is seen that for growth-promoting value as measured by

gain in weight, the following order holds: cornmeal and skimmilk, coconut oil meal, cornmeal and coconut oil meal, cornmeal. However, the differences are not marked except as between the skimmilk combination and the others. Inasmuch as food was given *ad libitum* and varied somewhat in amount for the different groups, as is indicated in the table, the better measure of growth-promoting value is, as has been previously pointed

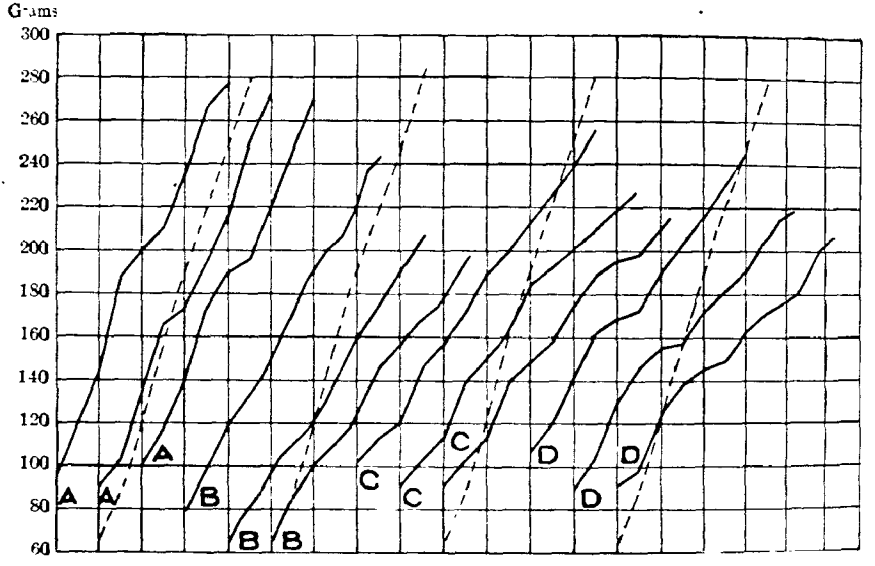

FIG. 74. GROWTH-PROMOTING VALUE OF COCONUT-OIL-MEAL PROTEIN AND CORN PROTEIN

A. Cornmeal protein 75 per cent, skimmilk protein 25 per cent. B. Coconut-oil-meal protein C. Coconut-oil-meal protein, 25 per cent, cornmeal protein, 75 per cent. D. Cornmeal protein The dotted curves represent the normal growth curve for the colony
The plane of protein intake is 9 per cent
The abscissas mark off periods of twenty days

out, the gain per gram of protein eaten. A consideration of these figures does not change the order given above, but the better quality of the protein in coconut oil meal as compared to that in cornmeal is much more evident. Coconut oil meal is seen to occupy an intermediate position, as regards growth-promoting value, between cornmeal and the mixture of cornmeal and skimmilk. The combination of cornmeal and coconut oil meal resulted in a value slightly above that caused by the former alone. This was due to replacing 25 per cent of protein of poor quality by protein

of better quality, but evidently there was no mutual supplementary action, since the growth-promoting value of the mixture was much poorer than that of the coconut oil meal alone.

TABLE 1. AVERAGE GAINS, TOTAL INTAKES, AND GAINS PER GRAM OF FOOD AND PROTEIN EATEN, SUMMARIZED BY PERIODS OF FOUR WEEKS (SERIES I)

Source of protein	Protein in foods (per cent)	Period	Average gain rat per (grams)	Total intake per rat		Gain per gram	
				Food (grams)	Protein (grams)	Food (grams)	Protein (grams)
Cornmeal	8 93	*T	5 8	85	7 59	0 068	0 76
		1	52 2	500	44 65	0 104	1 17
		2	22 7	548	48 94	0 041	0.46
		3	37 0	630	56 26	0 059	0 66
Totals			111 9±4 2	1,678	149 85	0 067	0 75
Coconut oil meal	8 99	*T	15 0	56	5 00	0 268	3 00
		1	39 6	374	33 62	0 106	1 18
		2	51 2	460	41 35	0 111	1 24
		3	41 7	468	42 07	0 089	0 99
Totals			132 5±7 6	1,302	117 04	0 102	1 13
Cornmeal and coconut oil meal, 75 25	8 93	*T	3 6	83	7 41	0 043	0 49
		1	48 9	526	46 97	0 093	1 04
		2	41 4	513	45 89	0 081	0 90
		3	25 6	571	50 99	0 045	0 50
Totals			115 9±4 7	1,610	143 85	0 072	0.81
Cornmeal and skimmilk, 75 25	8 93	*T	2 1	86	7 53	0 024	0 28
		1	87 1	512	45 69	0 170	1.91
		2	48 2	480	42 87	0 100	1 12
		3	45 5	568	50 73	0 080	0 90
Totals			180 8±1 7	1,560	139.29	0 116	1 30

*T represents the transition period of one week. Figures for the transition period are not included in the totals.

In series II, the ration of coconut oil meal and rice bran resulted in the best growth curves of the 9-per-cent-protein mixtures, causing a growth closely approximating the normal (fig. 75). It also gave the largest gain per gram of protein (table 2), and compared favorably in every respect with the cornmeal and skimmilk ration used in series I. When part of

the protein of coconut oil meal was replaced by protein from wheat middlings, a better growth resulted than on the former alone, and the gain per gram of protein was comparable to that resulting from the coconut-oil-meal and rice-bran ration. It must therefore be concluded that a protein mixture of higher quality results when coconut oil meal is supplemented with either rice bran or wheat middlings.

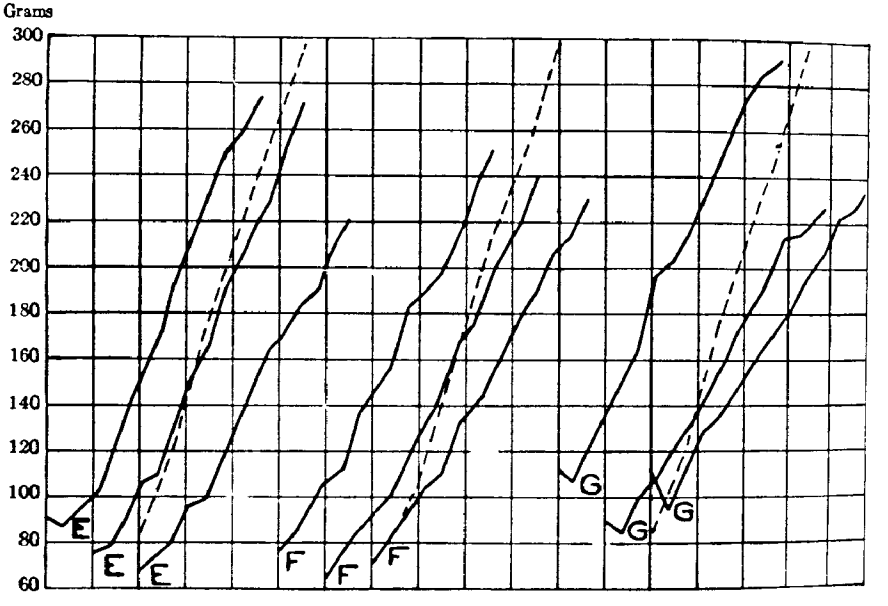

FIG. 75. GROWTH-PROMOTING VALUE OF COCONUT-OIL-MEAL PROTEIN SUPPLEMENTED WITH PROTEIN FROM VARIOUS OTHER FEEDING STUFFS

E. Coconut-oil-meal protein, 75 per cent, rice-bran protein, 25 per cent. F. Coconut-oil-meal protein, 75 per cent, wheat middlings, 25 per cent. G. Coconut-oil-meal protein, 75 per cent, kaffir-cornmeal protein, 25 per cent. The dotted curves represent normal growth.
The plane of protein intake is 9 per cent.
The abscissas mark off periods of twenty days.

The alfalfa-leaf-meal combination was obviously unpalatable, and the food intake was considerably lowered as a result, especially in the first few weeks. Hence the rats on this ration made a very poor growth at first, followed by a more rapid growth toward the end of the experiment when considerably more food was eaten. For the period as a whole, this combination proved scarcely as good as the coconut oil meal alone, with regard to both rate of growth and gain per gram of protein.

TABLE 2 AVERAGE GAINS, TOTAL INTAKES, AND GAINS PER GRAM OF FOOD AND PROTEIN EATEN, SUMMARIZED BY PERIODS OF FOUR WEEKS (SERIES II)

Source of protein	Protein in foods (per cent)	Period	Average gain per rat (grams)	Total intake per rat		Gain per gram	
				Food (grams)	Protein (grams)	Food (grams)	Protein (grams)
Coconut oil meal and rice bran, 75 25	8 99	*T	1 4	64	5 75	0 022	0 24
		1	47 9	392	35 24	0 122	1 36
		2	70 8	541	48 64	0 131	1.46
		3	58 5	527	47.38	0 111	1.23
Totals .			177 2±11 5	1,460	131 26	0 121	1 35
Coconut oil meal and wheat middlings, 75:25	8 99	*T	11 2	64	5 75	0 175	1 95
		1	46 5	365	32 81	0 127	1 42
		2	53 1	464	41 74	0 114	1.27
		3	59 1	513	46 12	0 115	1 28
Totals.			158 7± 5 7	1,342	120 67	0 118	1.32
Coconut oil meal and kaffir corn, 75.25	8 99	*T	-10 4	70	6 30		.....
		1	50 9	491	44 14	0.104	1.15
		2	52 7	531	47 74	0 099	1 10
		3	45 0	472	42 43	0 095	1 06
Totals.		..	148 6±12 5	1,494	134 31	0 099	1.11
Coconut oil meal and alfalfa leaf meal, 75 25	8 99	*T	0 3	64	5 75	0 005	0 05
		1	36 9	350	31 47	0 105	1.17
		2	43 7	405	36 41	0 108	1.20
		3	37 7	440	39 57	0 086	0 95
Totals		.	118 3± 4 5	1,195	107 45	0.099	1 10
Coconut oil meal and alfalfa meal, 75 25	8 99	*T	8 5	98	8 81	0 087	0 96
		1	56 4	432	38 84	0 131	1 45
		2	61 3	538	48.36	0.114	1 27
		3	34 5	698	62 75	0 049	0 55
Totals		..	152 2	1,668	149 95	0 091	1 02
Coconut oil meal and rice bran, 75.25	14 84	*T	21 4	103	15 29	0 208	1 40
		1	100 3	487	72 27	0 206	1 39
		2	54 5	529	78 50	0.103	0 69
		3	44.5	477	70 79	0 093	0 63
Totals			199 3±13 6	1,493	221 56	0 133	0 90

*T [illegible] the transition period of one week. Figures for the transition period are not included in the totals

The alfalfa-meal combination was liberally consumed, and a better growth resulted than on the coconut oil meal alone; but this was accomplished with such a large intake of food that the gain per gram of protein was lower than that produced by the coconut oil meal alone. It may be noted in the chart (fig. 76) that only two individuals were in this group

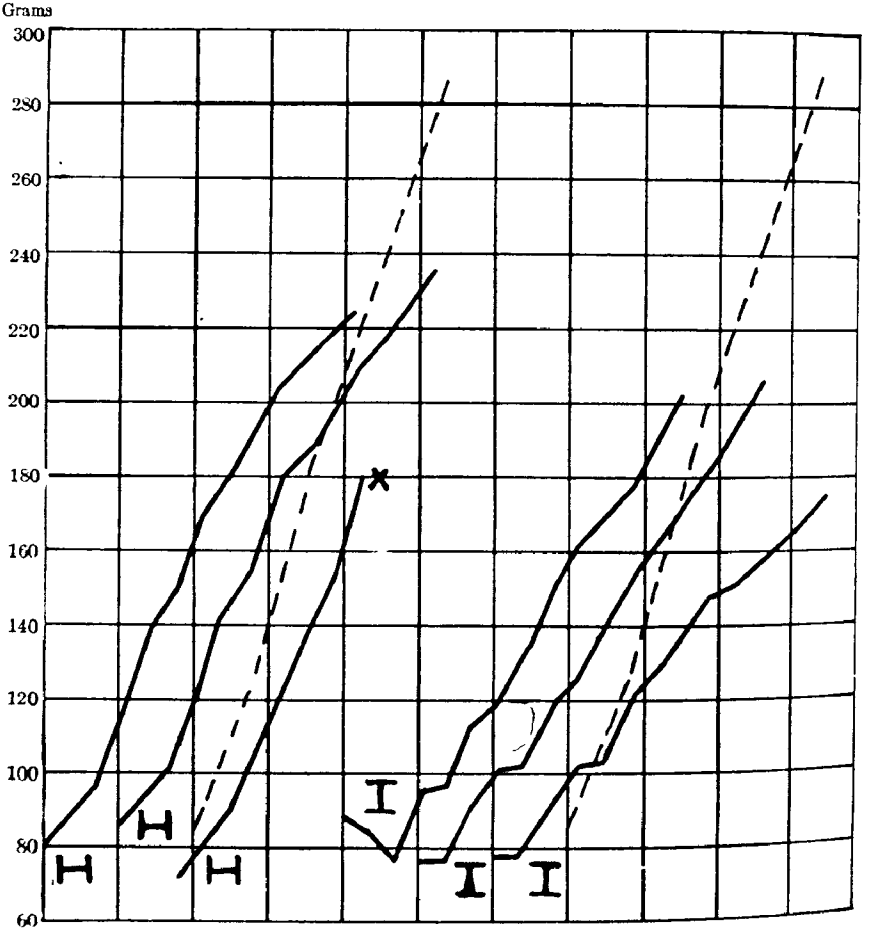

FIG. 76. GROWTH-PROMOTING VALUE OF COCONUT-OIL-MEAL PROTEIN SUPPLEMENTED WITH ALFALFA PROTEIN

H, Coconut-oil-meal protein 75 per cent, alfalfa-meal protein, 25 per cent. I, Coconut-oil-meal protein, 75 per cent, alfalfa-leaf-meal protein, 25 per cent. The dotted curves represent growth. The curve marked x in group H, represents a growth of nine weeks only, [illegible] accident, this rat was removed from the experiment at the end of that time.

The plane of protein intake is 9 per cent.

The abscissas mark off periods of twenty days.

during the third period. This fact, which prevented computation of the probable error of the mean gain, limits the value of these calculations relative to gain per unit of food and protein eaten, and thus affects the definiteness of these conclusions. Difficulty was experienced also in keeping an accurate account of food intake on this ration, because it was scattered somewhat, despite all precautions. It must be considered that the trials with both the alfalfa products are rather unsatisfactory. It is hoped that further studies will be made of the question of the supplementary action of the protein of roughage and that of grain, since knowledge regarding this question is of great importance for the formulation of rations for farm animals.

The combination of kaffir corn with coconut oil meal resulted in no marked advantage over the latter alone as regards rate of growth, and no increase in the gain per gram of protein. Hence the addition of kaffir-corn protein does not improve the protein of coconut oil meal.

The trial with coconut oil meal and rice bran at a 15-per-cent plane of protein intake furnished further evidence as to the high quality of this combination. Normal growth resulted, as is shown in figure 77. This was rather to be expected in view of the results obtained with the same combination containing 9 per cent of protein. The gain per gram of protein was not as great as at the 9-per-cent protein intake, and this is expected. The work of Osborne, Mendel, and Ferry (1919) indicates that for a given source of protein the maximum gain per gram results on a plane of intake which is below that required to furnish normal growth. Inasmuch as the 15-per-cent plane of intake was at least sufficient for normal growth, it could not be expected to give as great a gain per gram of protein.

It is to be noted in the charts that the gains within a group were for the most part fairly uniform. This uniformity within the groups justifies, it is believed, the significance herein attached to the differences between the groups. A consideration of the probable errors listed in the tables strengthens this view. Inasmuch as individual food-intake records were not kept, the calculations for the gain per gram of food and protein eaten are subject to an indeterminate probable error, governed by the variation in individual intake. It is not believed, however, that this variation would be large for rats of the same weight making uniform gains, inasmuch as food intake is fairly closely regulated by calorific requirements.

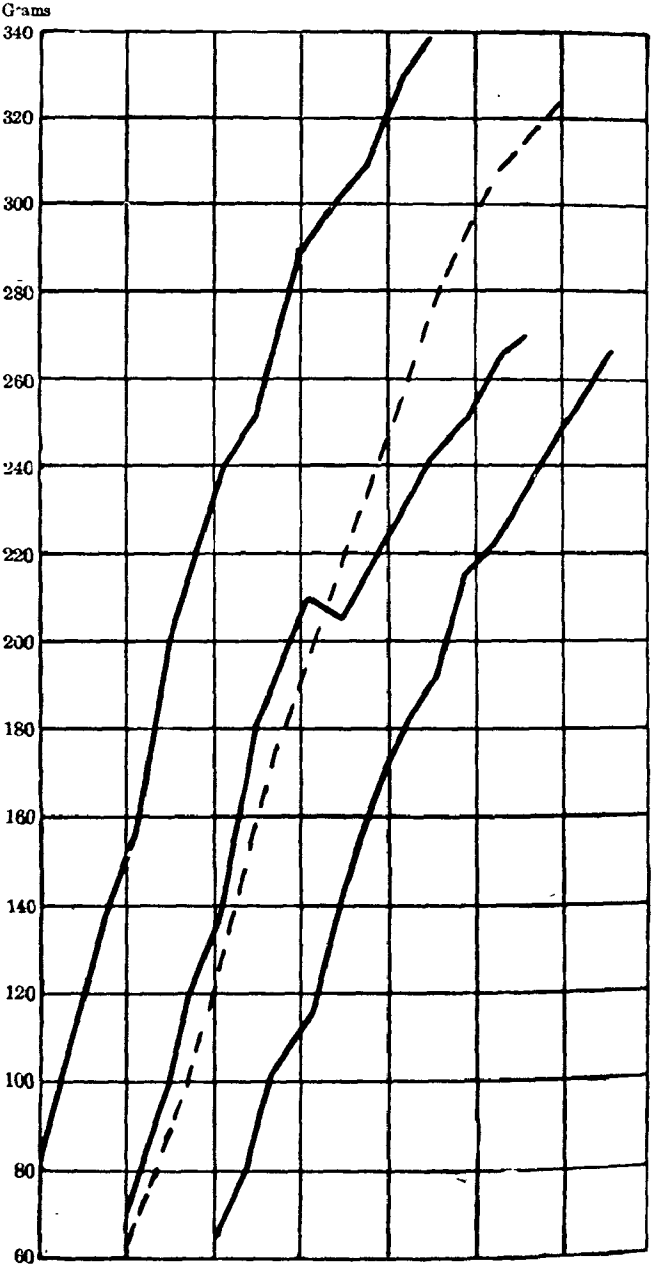

FIG. 77. GROWTH-PROMOTING VALUE OF COCONUT-OIL-MEAL PROTEIN AND RICE-BRAN PROTEIN IN THE RATIO 75:25, AT A PLANE OF INTAKE OF 15 PER CENT

The dotted curve represents normal growth. The abscissas mark off periods of twenty days

SUMMARY

The protein of coconut oil meal was found to be of higher quality than that of cornmeal. A mixture of cornmeal protein and coconut-oil-meal protein was of slightly higher quality than the former alone, but much poorer than the latter alone.

Both rice bran and wheat middlings proved effective supplements to coconut oil meal. At a plane of intake of 9-per-cent protein, coconut-oil-meal protein supplemented with 25 per cent of rice-bran protein was equal, in rate and economy of growth caused, to the high-quality combination of cornmeal and skimmilk, in which 25 per cent of the protein of the former is replaced by the latter.

The trials in which coconut oil meal was supplemented by alfalfa products were not very satisfactory, but the data obtained indicate that the resulting protein mixtures were of no higher quality than that of coconut oil meal alone.

The addition of kaffir corn to coconut oil meal resulted in no improvement of the quality of the protein.

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Manuscript, *Laboratory Experiments—II*, the ninth preceding number in this series of publications, was received for publication February 16, 1921.

ıBER, 1921 MEMOIR 51

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

ıE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ: ITS BIOLOGY, ANATOMY, AND HISTOLOGY

LAURA FLORENCE

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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THE HOG LOUSE, HAEMATOPINUS SUIS LINNE: ITS BIOLOGY, ANATOMY, AND HISTOLOGY

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ: ITS BIOLOGY, ANATOMY, AND HISTOLOGY[1]

LAURA FLORENCE

Because of their habitat on man and beast, lice have been known from the earliest times. Their systematic position has been a subject of controversy for more than a century, and the hog louse, on account of its large size and wide distribution, has frequently been used for the study of the morphology of the order. About the middle of the nineteenth century there was a controversy among physicians and entomologists as to the nature of the mouth parts of the pediculi infesting man, and the mouth parts of the hog louse were brought into the discussion by Burmeister. A detailed account of this discussion is given in a paper by Schjodte (1864, English trans. 1866: 213). Since the pediculi infesting man have been shown to be an etiological factor in the transmission of certain diseases, much accurate work has been done on their life history and morphology, and the many points of interest raised through such detailed study suggested that a parallel study of an animal parasite might be equally profitable. The aim of the present work has been to give an accurate account of the general internal anatomy of the hog louse, with a detailed description of the histology of certain parts. The relation between the parasite and its host has not been considered, and references to veterinary literature do not appear in the bibliography.

The study was begun in 1917 in the Entomological Laboratory of Cornell University under Dr. William A. Riley, now of the University of Minnesota, and was continued under Dr. O. A. Johannsen, to both of whom thanks are due for helpful criticism. Since June, 1918, by the courtesy of the Scientific Directors of the Rockefeller Institute, and, in particular, of Dr. Theobald Smith, Director of the Department of Animal Pathology, it has been made possible for the writer to complete the investigation

[1] From the Department of Entomology of the New York State College of Agriculture at Cornell University, and the Department of Animal Pathology of the Rockefeller Institute for Medical Research. Also presented to the Faculty of the Graduate School of Cornell University, June, 1920, as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

HISTORICAL REVIEW

According to Moufetti (1634, English trans. 1658), the earliest reference to the hog louse is to be found in the works of Albertus, a writer of the twelfth century, who named the insect *Pediculus urius*. Moufetti retained this name and described the louse as somewhat larger than that infesting oxen and calves, and so hard that it could not be crushed between the fingers. Linnaeus (1758:291.5) described the louse under the name *Pediculus suis*. Panzer (quoted by Stevenson, 1905), in 1798, followed the nomenclature of Linnaeus and stated that in the classification of Fabricius this parasite was placed "with *Pediculus asini* of Redi (1671)." Leach (1817:65) broke up the genus Pediculus into four genera, Phthirus, Haematopinus, Pediculus, and Nirmus, making the hog louse the type of the new genus Haematopinus. This classification was not immediately accepted, and Nitzsch (1818:305) revived the old name of Albertus. He was followed in this by Burmeister (1839:58), who gave the synonymy and a brief description of the louse, and later (1847:569) gave a detailed description of the structure of the mouth parts.

Systematic descriptions and figures of the species are to be found in the monographs of Denny (1842.34), Giebel (1874.45), and Piaget (1880 654), of which the last is the most detailed. More recent and popular descriptions are given in three bulletins of the United States Department of Agriculture. Two of these are the work of Osborn (1891 and 1896), and in them the sections on the hog louse are identical. He calls attention to "a curious provision in the feet for strengthening the hold upon the hair, which does not seem to have been hitherto described." The third bulletin, written by Stevenson (1905), is valuable on account of the complete synonymy and the extent of the bibliography.

Between 1903 and 1906 a number of papers relating to the systematic position of the Pediculidae appeared in Europe. Most authors confined their investigations to the mouth parts, and for a time a bitter controversy was waged between Cholodkovsky of St. Petersburg and Enderlein of Berlin. Cholodkovsky (1903:120 and 1904:368) studied numerous sections of the head of the embryo of *Pediculus capitis*, while Enderlein (1904 and 1905), using cleared preparations and gross dissections, studied the hog louse in greatest detail of all the species used. Cholodkovsky's findings in regard to adult lice were confirmed by his pupil, Pawlowsky (1 . . 1.56), whose paper contains a discussion and criticism of the literature to date.

In the same year Gross (1903:347) published the results of his investigation of the ovaries of the Mallophaga and the Pediculidae. In his introduction he sums up an earlier investigation as follows:

> Handlirsch (1903) places them [the *Pediculidae*] in a special order Siphunculata, Meinert next the Mallophaga in his subclass Blattaeformia. Borner (1904) gives them the same name, but raises the family to the rank of a suborder which, together with the Corrodentia, the Thysanoptera, and the Rhynchota, forms his order of Acercaria. Cholodkovsky (1904) joins the dieuhidae and the Mallophaga in one order, related with the Orthoptera rather than with the Hemiptera, for which he proposes the name Pseudorhynchota. Finally, Enderlein (1904) interprets the Pediculidae as one with the Anoplura — a name originating with Leach — an order lying near to the Rhynchota. None of the four opinions mentioned is to be considered as entirely new. They are all found in similar form in the old entomologies of the preceding century.[2]

Gross next emphasizes the importance of using other less delicate organs than the mouth parts as a basis for comparison.

A historical review of lice from the time of Aristotle, together with an account of the general characteristics of the order and descriptions of species, was prepared by Von Dalla Torre (1908) for the *Genera Insectorum*. For this Enderlein's work served as a basis, as it did also later for the section on lice in the textbook of Patton and Cragg (1913:525). Neumann (1909:530) criticized Enderlein's splitting-up of the old genus Haematopinus of Leach as being for the present unnecessary, and retained the original classification in his descriptions of species (1911). Mjoberg (1910) published comparative studies of Anoplura and Mallophaga dealing with both the morphological and the systematic aspects of the question. Previous to this time only the dissertation of Strobelt (1882, English trans. 1883:73) had dealt with the anatomy of a species of Haematopinus — *H. tenuirostris*, now *Linognathus vituli*. The observations of the earliest workers — Hooke (1665), Swammerdam (1682), and Leeuwenhoek (1695) — and the investigations of the scientists of the latter half of the nineteenth century, dealt exclusively with the species infesting man. The presence of great armies in the field during the five years from 1914 to 1918, inclusive, compelled intensive studies of these species from medical and sanitary standpoints, with the subsequent publication of many valuable papers, of which a liberal use has been made in interpreting the anatomy of the species under investigation.

The classification followed throughout this paper is that suggested by Nuttall (1919:329) in a recent review of the systematic literature of the

[2] Translation from the original German.

Pediculidae. He points out that the order Anoplura Leach 1817 contains two suborders — Siphunculata Meinert 1891 and Mallophaga Nitzsch 1818 — and says (page 332 of reference cited): "Since, however, the name Anoplura Leach (1817) was applied to both Siphunculata and Mallophaga, and in this sense agrees with modern views, it should henceforth be used in its original sense only, there being no justification for continuing to apply it to Siphunculata alone."

BIOLOGY

The hog louse is the largest louse affecting domestic animals and is of common occurrence wherever the hog is found. The hog is its only host, and when not molested the parasite is likely to increase in large numbers and cause an unthrifty condition in a herd. The lice frequent the folds of the skin on the neck and the jowl, the inside and the base of the ears, the inside of the legs, the flanks, and, in smaller numbers, the back, where they crawl under the scales to get in contact with the new skin. They are well adapted for experimental work, because they are easy of access and feed readily on man, while their size and their habit of taking hold of any object placed in front of them lessen the difficulty of keeping them in confinement.

From the time of hatching, hog lice feed readily on man if they have not become weakened through too long fasting. During the course of this investigation hundreds of lice have been fed on the forearm without any resulting reaction, except, in a few cases, a slight redness which disappeared within half an hour, and, in cases in which the mouth parts were inserted but no blood was drawn, a slight swelling which disappeared within an hour. This is contrary to the finding of Sikora (1915 536), who saw no reaction on the first or the second day of the feeding but states that thereafter the skin turned red in an area from 1 to 5 millimeters around the point of puncture and swelled slightly, remaining thus for more than twenty-four hours. Recently Moore and Hirschfelder (1919 8) have published a detailed account of serious pathological effects of the bite of the clothes louse and clinical observations of the resulting illness. According to Stevenson (1905.12),

> Stockmen handling hogs often become temporary hosts of the louse, but it has never been known to remain for any length of time on the human body and is not known to exist on any animal other than the hog. Attempts made at this laboratory [United States Bureau of Animal Industry] to propagate *Haematopinus suis* on dogs have met with repeated failure.

Several attempts have been made to feed the lice on guinea pigs, but without success. The dense hair of the pigs hampers the movements of the lice, and, if shaving be resorted to, the lice are left without a foothold. If the finger be pricked and lice brought in contact with the freshly escaped blood, the lice immediately move away. Widmann (1915 b: 337) described a similar reaction in man-infesting lice, which refused to feed on various organs just removed from freshly killed mice.

When placed on the arm, hog lice may feed at once or may move about more or less rapidly. When walking they appear to move sideways as often as straight forward with the head in front. The peculiar structure of the feet, first described by Osborn (1891:20 and 1904: 107), enables the lice to grasp the hairs on the arm. The tibia (Plate LVIII, 1) increases at the distal end to twice the width of the proximal end, and the dorsal half only articulates with the tarsus. The remaining part is concave and its ventral border is drawn out to a spur, bearing a stout spine at the apex. In the concavity rests a stalked, protrusible, subcircular pad bearing two spines and two hairs. On the inner edge of the tarsus, in line with the surface of the extended pad, is a blunt process bearing a spine. The inner surface of the claw is slightly serrated. In holding a bristle or a hair, the claw is bent over to rest on the tibial spur and the pad is pushed against the opposite side of the bristle, thus preventing the insect from slipping. Enderlein (1904: 141), to whom Osborn's earlier description was evidently unknown, describes the pad as a strongly chitinized skeletal piece of triangular shape. In specimens cleared in potash and mounted under a cover glass it frequently has this shape, while in living and in uncleared specimens it always appears subcircular. Enderlein names this pad the *pretarsal sclerite*, which name is retained by Neumann (1911: 407) in his description of the insect.

The earliest description of a louse feeding is that of Hooke (1665:211-213). He described the passage of blood from his arm into a louse which he had placed there after it had fasted for several days, and the working of a pumplike apparatus in the head. Swammerdam (1682, English trans. 1758: 33-35) gave a more detailed description, but he disagreed with Hooke's description of the mouth parts, saying: "The louse has neither beak, teeth, nor any kind of mouth, as Dr. Hooke described it, for the entrance into the gullet is absolutely closed; in the place of all these, it has a proboscis or trunk, or, as it may be otherwise called, a pointed and

hollow aculeus or sucker, with which it pierces the skin, and sucks the human blood." He also described the pumplike structure in the head, the peristalsis of the alimentary tract, and the ejection of feces during feeding. Leeuwenhoek (1695) described the hook-bearing part of the proboscis and its eversion during feeding, in addition to other characteristic actions associated with the process.

When fed in captivity, the louse moves its head back and forth close to the surface of the arm and rapidly jerks the antennae up and down. Then, with the head held at right angles to the body, it seems to anchor itself to the skin, probably by the everted teeth of the haustellum. While the stylets are being inserted, the thorax and the abdomen are raised and gently rocked from side to side, and the claws make irregular scratching motions. After the insertion the insect is holding itself in a more or less straight line and at an angle of from 40° to 45° with the arm. As the feeding progresses the body is gradually lowered, until it rests on the arm and with its head forms an oblique angle. The act of sucking blood can best be watched in freshly molted specimens. The blood is first seen anterior to the eyes in the pumping pharynx, which dilates and contracts with great rapidity, driving its contents into the true pharynx (larynx of Enderlein), whence they disappear under the brain to reappear as a thin red line in the slender esophagus before this passes under the fat cells and muscle of the thorax. Throughout the process a continuous peristalsis passes along the whole alimentary tract, but this has manifestly no connection with the drawing of the blood, as suggested by Widmann (1915a, 290). It seems rather to be a means of removing from the posterior region of the stomach and from the intestine the débris of the preceding meal, since it is the habit of the hog louse — at any rate when kept and reared in captivity — to continue feeding until not only all the feces, but also a drop of blood, have been ejected. The latter may be pushed out by the interlocking of the six longitudinal folds of the epithelial lining of the intestine immediately behind the stomach, in order to prevent the escape of the blood from the mesenteron during digestion. At the first feeding after hatching, no blood has been seen to be ejected, and in some cases after the second feeding feces but no blood have been ejected. The average length of a meal is from eight to twelve minutes, but sometimes it lasts from twenty to thirty minutes, and at the close the mouth parts are apparently withdrawn by a short jerk of the head. Occasionally lice

have gorged themselves and have been seen to turn pink within a few minutes, owing to the rupture of the stomach and the spread of blood through the colon. This phenomenon, which has been invariably followed by death, has been seen also by Nuttall (1917 d:173) in the pediculi infesting man. The unfed louse is of a grayish color and much wrinkled, while the fed louse has a highly refractive, smooth tegument showing very clearly the areas of stronger chitinization. During keeping and rearing, immature lice have been given four, and adult lice three, opportunities for feeding in twenty-four hours, and these were not always taken advantage of. Temperature influences the rate of digestion, and the higher the temperature in which lice are kept, the more frequent must be the opportunities given them for feeding.

Sexual maturity is attained on the third day after the final molt, when, with or without fecundation, egg-laying begins. The position for copulation has been observed a number of times. While a female was feeding and still had the abdomen somewhat elevated, the male crawled underneath and interlocked his first and second pairs of legs with the second and third pairs of the female. She at once raised her abdomen, resting only on the head and the first pair of legs and bearing the whole weight of the male. The abdomens of both were curved dorsad and the male was seen to insert the parameres (dilator of Nuttall) into the sexual orifice of the female. Gradually the bodies were lowered until the third pair of legs of the male rested on the arm, and the head was under that of the female. They remained in this position for almost ten minutes, during which time the male constantly stroked the head of the female with his antennae. In its main features this resembles copulation in the pediculi infesting man as described by several workers, the most detailed account being that of Nuttall (1917 a:316). Hog lice in captivity have not been seen to remain in copulation longer than from ten to fifteen minutes, while the species infesting man crawl into hiding and remain so for several hours.

The eggs (Plate LVIII, 2) are laid, one at a time, on the bristles of the hog and are attached to them by a clear cement. They are most abundant on the lower parts of the body. The egg-laying process has been watched on the human arm during feeding. After drawing blood for almost ten minutes, the female withdrew the mouth parts but remained stationary, holding the end of the abdomen bent downward in an unusual manner.

Neither feces nor blood was ejected from the anus, but a drop of hyaline fluid escaped from the sexual orifice almost simultaneously with the pointed end of an egg. After a few seconds the louse moved away, leaving the egg attached to a hair on the arm. The position of the gonopods could not be seen, but the posterior lobes of the ninth abdominal segment surrounded the hair on which the egg was laid. According to Sikora (1915:536), who has described the act of egg-laying on a bristle by a hog louse in captivity in a vial, the insect remained motionless for almost ten minutes after the first appearance of the egg, and then moved off leaving the egg attached to the bristle. Watts (1918:9) says, "The entire operation requires but a few seconds, so that one seldom sees a female lay an egg unless watching closely for some time." In the ovaries the eggs are oriented according to Hallez' law, and, when laid, the ventral surface is attached to the bristle. The cement surrounds the bristle but does not appear to surround the egg, which is attached to the bristle between its transverse median line and its posterior end. One or more eggs may be laid on the same bristle, not always pointing in the same direction. After attachment we have always found them immovable, but Watts (1918:9) states that he has found they can be slipped along the hairs and are often pulled away from the body by the rubbing of the animal. This, however, does not agree with his earlier statement on the same page, that "each egg is glued to the base of a hair and is laid so that the smaller end practically touches the skin of the host, which keeps the egg warm until it hatches, several days later"; and, since the diameter of the bristle diminishes toward the tip, the cement ring large enough to surround the base of the bristle would tend to slip off, carrying the egg with it, thus causing an excessive mortality not provided for by overproduction.

In captivity the eggs are laid on bristles or threads of gauze, and the number laid daily appears to depend on the opportunity to feed, as the following table shows:

Opportunities of feeding in 24 hours	Number of eggs laid in 24 hours	Authority
Four	2	Sikora
Continuous	4	Sikora
Continuous for 7 days	3	Claassen[1]
Two	1 2	Florence

[1] Unpublished data kindly communicated to the writer by Professor P. W. Claassen, of the Department of Entomology, Cornell University

The last data relate to a female reared in captivity. Three days after the last molt, when put on the arm to feed, she moved rapidly about for thirty minutes, repeatedly elevating the posterior end of the abdomen, and made no attempt to draw blood. She was returned to the vial and two hours later was given another opportunity to feed, when an egg was found attached to a bristle in the vial. Twice a male was placed in the vial for some hours, but in neither case was copulation seen to occur. During a period of sixteen days eighteen eggs were laid, none of which hatched. The female died six days after laying the eighteenth egg, and gross dissection showed the ovaries very much shrunken. That oviposition continues without fecundation has been observed by various workers, and the unfertilized eggs are easily recognizable because they quickly change color and shrivel up.

When laid, the egg is an iridescent pearly white. As development progresses it becomes more opaque, and toward the end of the incubation period it appears light amber in color. Its average length is 1.5 to 1.75 millimeters, and its average breadth at the widest part is 0.5 to 0.75 millimeter. It is symmetrical, tapers posteriorly, and is bluntly rounded at the anterior end, where the operculum is situated. The widest part is just behind the operculum (Plate LVIII, 2). The surface is covered with small punctations, which are somewhat larger on the operculum than on the main part of the egg. The junction of the egg with the operculum is indicated by a small ridge bearing striations parallel to the longitudinal axis of the egg.

Hatching has not been observed, but eggs have been seen shortly after being hatched. The operculum opened away from the bristle and remained attached to the egg by a small hinge; protruding from the egg was a small fragment of the vitelline membrane (Plate LVIII, 2). A number of authors have mentioned points in connection with the hatching of pediculi infesting man, and Sikora (1915:530) was the first to give a short description of the process, which has since been confirmed and extended by Nuttall (1917 d 148). Probably in the hog louse the process is essentially the same. The following data show that the period of incubation is influenced by temperature, and suggest a reason for the seasonal variation in the development of the eggs on the hog:

Condition	Eggs hatched after	Authority
On hog	About 5 days	Coburn[4]

[4] Data of Coburn (1888).

Conditions	Eggs hatched after	Authority
On hog	From 13th to 20th day, maximum about 16th day	Watts
Room of ordinary humidity, at temperature of 85° F., in September	From 15 to 16 days	Stevenson
Same conditions, but eggs kept in a closed dish containing a receptacle filled with water	12 days	Stevenson
Temperature by day of 26° C. and by night of 35° C.	17 days	Sikora
Incubator at constant temperature of 37° C., dry heat	11 to 12 days (5 eggs hatched, out of 24)	Florence
In vials, worn constantly next the body	14 days (9 eggs hatched, out of 19)	Florence
Conditions as in last preceding	13 days (4 eggs hatched, out of 5)	Florence

The period of incubation evidently lies between twelve and twenty days, with a minimum period of about thirteen to fourteen days when the eggs are kept constantly at body temperature. It is interesting to compare this with the recent work of Bacot and Linzell (1919 388), who found the incubation period of the eggs of the horse louse, *Haematopinus asini*, to be apparently from sixteen to twenty days, and the minimum period under natural conditions about fifteen to sixteen days.

In the course of their development hog lice undergo three molts, and rearing in captivity has proved the cycle from egg to egg to occupy from twenty-nine to thirty-three days. The life history, as we have observed it, is summarized in the following table:

Time from laying to hatching of eggs	13 to 15 days
First molt occurred after	5 to 6 days
Second molt occurred after	4 days
Third molt occurred after	4 to 5 days
Sexual maturity occurred after	3 days

Time of development from first-stage larva to mature adult	16 to 18 days
Temperature and other conditions	35° C., continually next to body, in vials
Number of feedings in 24 hours	1 to 4
Duration of cycle from egg to egg	29 to 33 days

THE EARLY STAGES

The newly hatched louse has 5-segmented antennae and a 9-segmented abdomen, as are found in the adult. The claws and the pad, already described, are present as in the adult, but no joint between the tibia and the tarsus appears until after the final molt (Plate LVIII, 1 and 5). Attention was drawn to this point by Gillette in his brief description of the species written for Coburn (1912:497). The head is large in proportion to the almost colorless body. Only the claws, and the sides of the head in the region of the clypeus, show marked chitinization. During the first instar (Plate LVIII, 3) the dark color gradually extends along the lateral and posterior dorsal regions of the head and the thorax, the legs become more strongly chitinized, and there is some indication of the transverse abdominal plates. The chitinous plates of the pleurites are represented by small, light brown spots close to the spiracles. In the second instar (Plate LVIII, 4) the chitinization is generally more marked, but the buccal tube can still be clearly seen through the integument. The transverse abdominal plates are more developed, the plates of the pleurites are approximately four times as large as in the first instar, and between these two are small circular chitinous areas. In the third instar (Plate LVIII, 5) the head is more strongly chitinized and the buccal tube can no longer be seen throughout its length. The plates of the pleurites resemble those of the adult but are somewhat lighter in colour. The ninth abdominal segment shows no chitinization but is turned slightly dorsad, and the first antennal segment, which in the previous stages was almost of the same diameter as the four other segments, is now considerably larger than these. At the third molt the chitinous plates, which are the external indications of sex, appear at the posterior end of the body. In both male and female, maturity is indicated by a sternal chitinous plate which appears on the thorax about the third day after the final molt (Plate LVIII, 6). The

mature female averages about 4.6 millimeters long by 2.19 millimeters at the broadest part of the abdomen, and the male averages about 3.9 millimeters long by 2.1 millimeters broad. The following table gives the average measurements throughout the life history:

Age	Instar	Number of feedings since preceding molt	Length (millimeters)	Breadth (millimeters)
Newly hatched	1	0	1.00	0.50
12 hours	1	3	1.25	0.50
7 days	2	(?)	1.75	0.75
8½ days	2	8	2.25	1.00
9¾ days	3	1	2.50	1.00
10½ days	3	3	2.75	1.25
14 days	4	1	3.00	1.25
15¾ days	4	4	3.25	1.50
18 days	4	2	4.00	2.00
Mature female			4.60	2.19
Mature male			3.90	2.10

In immature lice the lines along which the tegument ruptures at molting are very distinct. When about to molt the insect raises itself until only the posterior end of the abdomen, and the claws of the second pair of legs, are touching the surface on which it rests, the back has a humped appearance, and the head is bent downward at right angles to the body. The first rupture is along the dorsal median line of the thorax and gradually extends caudad to the fifth or sixth abdominal segment and cephalad to the frons, where it divides, passing to the base of each eye. Air is sucked up into the pharynx and passes through the alimentary canal to escape at the anus. The body is inflated, pushed through the dorsal ruptures, and so drawn away from the old skin. The body is lowered until it touches the hair or bristle on which the louse is resting, when the legs are folded laterally across it and the ventral surface of the thorax and the abdomen (Plate LVIII, 7). The head and the thorax are gradually drawn upward until the eyes and the proximal segments of the antennae are seen, disclosing at the same time on the old skin a ventral T-shaped rupture, the stem of the T lying along the median line from a point midway between the bases of the antennae to the prosternum, where there is a

transverse split; the chitin on each side of the median rupture is stretched back so that the opening resembles a triangle. The first pair of legs is next withdrawn, and these, pushing down the skin, help in the final freeing of the head and the mouth parts. These now occupy their normal position, and the second and then the third pair of legs are withdrawn, pushing the insect forward and freeing it from the old skin, which remains anchored to the surface upon which the insect has emerged. The process took place when a louse had been put on the arm to feed and was watched through a binocular. From the first rupture of the old skin until the complete emergence of the insect, thirty minutes elapsed; Sikora (1915: 525-526) describes the process in *Pediculus vestimenti* as lasting but five minutes. No description of the act has been found in the literature of the hog louse, and the slowness in the case observed may have been due to the unnatural environment of the insect; moreover, death followed within an hour of molting.

THE ADULT LICE

The male and the female are recognized by their difference in size, the shape of the abdomen, and the structure of the two posterior abdominal segments. Both are without pigmented eyes, but the projections on the sides of the head have a lateral, slightly convex, refractive surface suggestive of a lens. While the thorax of the female is somewhat shorter and broader than that of the male, the legs of the sexes are identical, showing no modifications for clasping in relation to copulation. No constant variations in pigmentation have been observed.

THE MALE

The abdomen of the male is considerably shorter than that of the female, so that, although it measures the same or even slightly less in its widest region, it appears considerably broader. The tergites of segments 1 and 2 are small, but clearly defined. Hairs are present in each abdominal segment in a transverse row. Posteriorly the abdomen is rounded; the terminal segment curves dorsad and anterior, bringing the rectal and sexual orifices into a dorsal position (Plate LVIII, 8). On the ventral surface there is a strongly chitinized plate of characteristic shape extending from the transverse median line of segment 7 through segment 8 to segment 9, its posterior edge being visible from the dorsal aspect of the

abdomen. Anterior to this plate, in segments 7 and 6, the anterior end of the basal plate can be seen shining through the integument (Plate LVIII, 9).

THE FEMALE

In the female, as already said, the abdomen is longer than in the male, and in consequence it appears more slender. The tergites of segments 1 and 2 are similar to those of the male. Hairs are fewer in number and arranged with much less regularity. The ninth segment has a deep indentation on the posterior median line, and the lateral regions are modified into rather blunt, strongly chitinized processes pointing inward and slightly ventrad, apparently a modification for clasping the bristle during egg-laying, and, according to Mjöberg (1910.216), not unusual in Siphunculata (Anoplura). On the dorsal surface of the segment there is a strongly chitinized plate extending onto each projection, and between it and the edges of the indentation is a row of stout hairs (Plate LVIII, 10). On the ventral surface the gonopods lie on segment 8. They present a striking contrast to those of the pediculi infesting man, in that they are quite flat and lie widely apart. They are flat processes, narrowing posteriorly, and their median free border is somewhat strongly chitinized and set with a row of stout hairs. Anteriorly they are joined by a fold of the integument which projects caudad in two blunt points (Plate LVIII, 11). They have arisen, apparently, as an infolding of the integument of the segment, and may be considered homologous with the gonopods of the Trichodectidae as described by Morse (1903.609).

THE INTEGUMENT AND BODY WALL

The integument is tough rather than hard, and chitin is well developed only in certain clearly defined regions. Sculpturing of the cuticula, described by Mjöberg (1910.185) as typical of most Siphunculata (Anoplura), is absent from this species. In the head the cuticula is strongest along the sides, where the muscles controlling the backward movements of the pharynx are inserted, and in two transverse bars — one in the region of the clypeus, where the muscles of the pumping pharynx are inserted, and a second in the frons, where the muscles of the true pharynx are inserted.

Where the head passes into the thorax a ring of chitin forms the neck, and from its median dorsal surface two chitinous processes extend into

the thorax. These were described in this and other Siphunculata (Anoplura) by Enderlein (1904:126), who named them "Hinterhauptvorsatz" and thought that morphologically they probably originated as tendons of the retractor muscles of the head. Mjöberg (1910:202-203) named them the "occipital apodeme." Gross dissection reveals the continuation of these processes as muscle bands having their origin on the apodeme of the metathorax, while muscles controlling the lateral movements of the head are inserted on their posterior lateral borders.

The dorsal surface of the thorax is strongly chitinized and the segments are completely fused with one another. In mature lice the sternal plate is present on the ventral surface. On the prothorax, and also on the anterior angles of the sternal plate, is a pair of very small openings approximately 0.03 millimeter in diameter, which are present at all stages of development (Plate LVIII, 6, 8, and 10) and have been passed over or variously described up to the present time. Stevenson (1905:15), in his description of the thorax, says: "On the ventral surface between the appendages is a chitinous shield. In each anterior lateral angle of this shield or plate is an opening called the osteole, leading from a canal that extends cephalad." Mjoberg does not mention either of the pairs of openings, and Neumann (1911:407) describes "a pair of very small thoracic stigmata"[5] and "a small stigma in each anterior angle"[5] of the sternal plate. Patton and Cragg (1913:548) describe both pairs of openings as stigmata. On the sternal plates of seventeen species of Siphunculata (Anoplura) figured by Kellogg and Ferris (1915: Pl. IV), no such openings are present.

Gross dissection has shown that these openings are quite different from the stigmata of the tracheae, are without a closing device, and communicate with a canal which has no connection with the respiratory system. The dorsal openings on the prothorax are connected with those on the sternal plate by a rigid, uniformly chitinous canal passing directly dorsoventral laterad of the thoracic tracheal trunk. One short branch is given off almost at right angles to the main stem and at about one-third of the total length of the latter from its dorsal surface, and passes caudad terminating in the transverse band of muscle which lies between the second pair of legs (Plate LVIII, 12). Series of cross sections made through the

[5] Translation from the original French.

thorax at various angles after impregnation of the tissue with silver chromate proved conclusively that the structure has no connection with the tracheae and that the canals are unmodified ingrowths of the body wall. They are composed of chitinous cuticula covered with a layer of small hypodermal cells, and form a rigid internal frame, analogous to the skeleton of higher animals, for the partial support of the muscles of the first and second pairs of legs and a transverse muscle of the thorax. No communication between these and a canal extending cephalad, as described by Stevenson, has been found. They are to be regarded as a paired apodeme of the prothorax and the prosternum.

In the region of the metathorax on the median line there is a marked ingrowth of the cuticula, which forms the center of a ridge-like thickening on the inner surface of the segment. This ridge serves for the insertion of the muscles of the neck, the legs, and the dorsal abdominal plate, and may be named the *metathoracic apodeme*. In the abdomen the segmentation is clearer on the dorsal than on the ventral surface. Segments 1 and 2 are small and have the appearance of belonging to the thorax. As already said, these tergites are clearly defined in both sexes. Segments 3 to 8 have strongly chitinized plates on the pleurites and moderate chitinization of the tergites, while the sternites are almost colorless. The primary cuticula is very thin and can be dissected off with ease from the secondary cuticula, which is of a leathery consistency and in sections has a striated appearance as if deposited in layers. When stained with hematoxylin and eosin the secondary cuticula stains pink except in the strongly chitinized regions, where the primary and secondary cuticulae both retain their yellow color.

The hypodermis underlying the cuticula is made up of uniform cells which become longer and more slender on either side of the trachogen cells. The latter are considerably larger than the hypodermal cells and their basal part is subcircular, and in some cases multinuclear sensory cells lie alongside them sending a prolongation into the hair.

THE RESPIRATORY SYSTEM

Hooke (1665) saw numerous tracheae intimately connected with the fat cells of the louse, but did not recognize their true function. Swammerdam (1682, English trans., 1758:32) saw seven pairs of stigmata with their tracheae. He described their structure and their numerous branches

passing among the viscera, pointing out the resemblance between them and the windpipe of man. Landois (1864:12, 1865 a:45, 1865 b:499) gave the first complete descriptions of the general respiratory system, describing in detail and figuring the closing apparatus of the tracheae of Phthirius. Then followed Ströbelt's (1882:106) description of *Linognathus vituli* (*Haematopinus tenuirostris*). Both writers agreed in the general arrangement of the tracheae and the number of stigmata, but considered those of the abdomen as being situated on segments 2 to 7, an opinion held earlier by Denny (1842:34) and later by Stevenson (1905:15) and by Neumann (1911:407). Mjöberg (1910:218) described the general system for Siphunculata (Anoplura) and compared it with that of Mallophaga. Harrison (1916a:191) worked on the respiratory system of the Mallophaga, and used Siphunculata (Anoplura) for comparative purposes. His results confirmed the earlier work of Mjöberg, who had pointed out the marked resemblance between the Siphunculata (Anoplura) and the less specialized forms of the Mallophaga. In the same year Muller (1915.29-32) described and figured the respiratory system in the clothes louse.

In the hog louse there are fourteen stigmata, the typical number for Siphunculata (Anoplura) — one pair on the thorax in line with the second pair of legs, and six pairs on segments 3 to 8 of the abdomen. The abdominal stigmata on segments 3 to 6 lie on the dorsal transverse median line, while those on segments 7 and 8 are more posterior and lateral in position and can be seen from both dorsal and ventral aspects. The stigmata are slightly raised above the integument and are surrounded by a stout chitinous band, the peritreme. The thoracic stigmata are oblong-ovate, measuring from 0.06 to 0.07 millimeter at the widest part, and the abdominal stigmata are circular, with a diameter of about 0.05 millimeter.

The respiratory system (Plate LIX, 1) consists of two lateral tracheal trunks extending the whole length of the insect, a posterior abdominal commissure, and four more slender commissures in connection with the main ganglia. In the abdomen the main tracheae lie near the dorsal surface on either side of the alimentary tract, and are united posteriorly in segment 8 by a commissure of diameter equal to their own, from which numerous fine branches pass to the fat cells of segment 9. In segments 8 to 3 a branch is given off from each main trunk to the stigmata of the segment and they in turn each send off two slenderer branches which,

breaking up into innumerable tracheoles, pass through the lateral muscles and support the digestive and reproductive organs from their ventral aspect. Between segments 7 and 3, eight branches are given off centrad from the lateral trunks. These pass to the dorsal muscle plate, the heart, the dorsal fat cells, and the surface of the alimentary tract.

In some species, roots of branches extending laterad from the main trunks, between the branches to the stigmata of segment 3 and the thorax, have been described by investigators who have regarded them as vestiges of branches to the lost stigmata of segments 1 and 2. Such roots have not been found in this case. In the region of the second segment two slender branches are given off, one laterad and the other centrad. The former soon bends downward and breaks into numerous tracheoles on the surface of the salivary glands, while the latter ramifies among the fat cells on the dorsal anterior region of the stomach. Under the sternite of the first segment a slender branch comes off from each main trunk and passes to the dorsal surface of the stomach, and a second fine branch arises where the main tracheae bend somewhat ventrad as they pass into the thorax. This branch breaks up in the thoracic muscle of the third pair of legs.

In the thorax the main tracheae bend underneath the muscles coming from the legs to the metathoracic apodeme. In line with the third pair of legs a very short branch is given off laterad, from the posterior side of which arise two branches, one passing directly into the leg, and the other centrad for a short distance, when it divides into three parts. The first part of this branch is the commissure of the metathoracic ganglion, the second ramifies on the ventral wall of the stomach, and the third bends laterad passing into the leg. Opposite the second pair of legs is a tracheal plexus, from which spread six large branches as well as many small branches supplying the surrounding muscles and fat cells. A stout dorsal branch connects the plexus with each thoracic stigma. The first branch going cephalad divides, one part passing laterad to the first pair of legs, the other passing centrad as the commissure of the prothoracic ganglion, first giving off a branch which turns backward and supplies the first pair of legs. The second branch going cephalad is a continuation of the lateral tracheal trunk and passes to the head. A branch passes directly centrad as the commissure of the mesothoracic ganglion, and from it a branch arises at the lateral border of the ganglion and bends

around, passing into the second pair of legs. The fifth branch leaves the plexus almost at the same point as the preceding, turns back, and enters the main trunk centrad of the point of issue of the tracheae of the third pair of legs, thus forming a loop, which may correspond to the thoracic tracheal triangle described by Harrison (1916 a:105) in some Mallophaga. There, however, the thoracic stigma forms the apex of the triangle, while this loop lies behind the stigma. Harrison suggests that the inner side of the triangle may be the only survival of wing tracheae. The sixth branch comes from the branch to the thoracic spiracle just dorsad of its entrance into the main trunk, and passes into the second pair of legs. As has been shown, two tracheae pass into each leg, one of which lies ventral and the other dorsal. In the coxae, branches are given off which break up into many fine tracheoles; in the femur a large branch is given off from each trachea, and one of these branches passes along with the main branches into the tibia, where the latter subdivide many times, passing into the spur, the pad, the tarsus, and the claw.

The main trunks, on leaving the tracheal plexus, bend centrad and dorsad, passing into the head on either side of the esophagus and the aorta directly under the occipital apodeme. Just behind the sub-esophageal ganglion they diverge, and shortly give off a lateral branch to the neighboring muscles. Behind the brain a branch is given off centrad, and from its root the commissure of the sub-esophageal ganglion issues, while it passes forward close to the lateral borders of the brain. The main trunks continue forward alongside the antennal nerves, give off a branch to each antenna, and break up into numerous branches among the glands, the fat cells, and the sensory cells of the anterior region of the head.

The external surface of the stigma resembles a cart wheel with an open hollow axis, and sections show the vestibule between the stigma and its trachea to be filled with hair-like, chitinous structures radiating from its inner surface to a thin wall surrounding a slender central canal (Plate LIX, 3). These spoke-like projections doubtless prevent the entrance of foreign particles along with the air. A similar structure has been described by Muller (1915:30) in the clothes louse. Between the vestibule and the trachea is inserted the closing apparatus, concerning the mechanism of which there is still some uncertainty. Krancher (1881:522–533) briefly described the structure in *Haematopinus suis*. His figure shows the nature of the vestibule, the closing lever, and one intrinsic muscle between

the free end of the lever and the wall of the trachea opposite the attachment. No further description appeared until that of Mjöberg (1910:221), who figures a single muscle attached to the free end of the lever, and describes its insertion in the body wall near the stigma. At the close of a detailed study of the stigmata of Heteroptera and Homoptera, Mammen (1912:172) divides insect stigmata into four groups, according as they have one extrinsic muscle, one intrinsic muscle, two muscles, or three muscles, connected with the closing apparatus. Harrison (1916a:116) gives a brief résumé of the literature on the subject. He finds in Siphunculata (Anoplura) and in Mallophaga two muscles, which may be homologous with the "Musculus constrictor" and the "Musculus tendinosus" described by Solowiow (1909:707) in the caterpillar of *Cossus cossus* L. Müller (1915:30) refers to Landois' work on Phthirius, and says that he himself could get no clear picture of the structure in *Pediculus vestimenti* from the study of sections.

Study of the hog louse has revealed a closing apparatus resembling that of *Heterodoxus longitarsus* as figured by Harrison (1916a:116), who describes it as an intermediate type and gives no account of the musculature. The thoracic and abdominal stigmata are essentially the same in structure and in mechanism, but the vestibule of the thoracic stigmata is somewhat shorter, measuring approximately 0.08 millimeter from the surface of the stigma to the closing lever, while that of the abdominal stigmata (Plate LIX, 3) measures 0.11 millimeter. The approximate diameter of the vestibule of the abdominal stigmata is 0.03 millimeter, and at its inner end it narrows and both walls become strongly chitinized. A chitinous lever about 0.03 millimeter long is attached to the ventral wall, and the dorsal wall projects into the lumen as a sharp point. Beyond the lever the wall continues strongly chitinized and somewhat convex for a distance of about 0.016 millimeter, when it passes into the trachea proper. This region corresponds to the bulla of Harrison. In gross dissections no muscles have been found (Plate LIX, 2), but from the study of sections cut at various angles there appear to be two muscles arising from the free end of the lever. One of these is inserted in the convex wall of the bulla, and the other in the body wall just dorsad of the stigma. This agrees with the findings of Harrison in other Siphunculata (Anoplura) and in the Mallophaga. He offers two interpretations of the structure: (1) both the extrinsic and the intrinsic muscle function in closing the

stigma, or (2) closing is effected by the intrinsic muscle and reopening by the extrinsic muscle. With Harrison, we consider the former the more reasonable explanation, in which case it is assumed that the trachea opens through its own elasticity on the relaxing of the closing muscles.

THE MUSCULAR SYSTEM

With the exception of Osborn's (1904) note on the musculature of the protrusible disks and the claw, nothing has been published concerning the muscular system of the hog louse, and the only work on an allied species is that of Ströbelt (1882, English trans. 1883:100) on *Linognathus vituli* (*Haematopinus tenuirostris*). Landois (1864–22, 1865 a:33, 39, and 1865 b 495) described and figured a part of the musculature of the species affecting man, and was the first to observe the arrangement of the muscles in the female. Recently Muller (1915–10) has confirmed the work of Landois and has described in addition the arrangement of the muscles in the male. Nuttall (1917 a:295) has briefly mentioned and summarized the different arrangement of the abdominal muscle plates in the two sexes as described by Landois and Muller. The musculature of the hog louse presents some striking contrasts to that of the pediculi infesting man.

The head contains many muscles, of which the majority control the pharynx and the mouth parts and are described later in connection with those parts. The muscles controlling the antennae are confined to the head and the first segment of the antennae, those in the head all originating in the dorsal wall and none of them in the ventral as in the pediculi infesting man. There are six muscles, which originate in close succession on either side of the dorsal median line above the frontal ganglion and immediately posterior to the elevator muscles of the pumping pharynx. The two anterior muscles pass obliquely backward and downward, and are inserted in the ventral articulation of the antennae with the head; the two median muscles pass almost directly ventrad and are inserted in the dorsal articulation of the antennae with the head; and the two posterior muscles pass obliquely anterior and downward and are inserted immediately posterior to the median muscles. In the antennae the muscles are confined to the first segment, and consist of four bundles originating at the articulation of the antennae with the head and inserted two in the anterior and two in the posterior articulation of segments 1 and 2.

The muscles controlling the movements of the head lie in the anterior part of the thorax and have their origin in the metathoracic apodeme and in the strongly chitinized tergite of the prothorax. The elevator and retractor muscles are six in number and originate in the metathoracic apodeme, three on either side of the median line; the two median muscles are inserted in the distal ends of the occipital apodeme, and the two lateral muscles on either side pass cephalad and are inserted in the neck. The two depressor muscles are made up each of three strands, and originate in the dorsal wall of the prothorax on either side of the elevator muscles on the transverse median line of the first pair of legs. They pass obliquely ventrad and cephalad, and are inserted as two short, stout tendons in the chitinous ring of the neck on either side of the ventral median line. The lateral movements are controlled by muscles made up each of four strands. They originate in the dorsal wall of the prothorax laterad of the depressor muscles, and pass obliquely centrad, where they are inserted in the lateral borders of the prongs of the occipital apodeme at its distal end.

The muscles controlling the legs originate in the metathoracic apodeme, and if the dorsal surface of the thorax be carefully removed or if horizontal sections be made through this region, the muscles are seen to have a stellate arrangement with the apodeme as the center point of the star. A similar condition exists in the pediculi infesting man, and has been figured by Müller (1915). There are in all eighteen groups of muscle strands originating in the apodeme, and three of these groups are inserted as stout tendons — two in the dorsal articulation of the coxa with the thorax, and one a short distance within the ventral wall of the coxa, in each leg. Each group is composed of some five to seven strands, which vary in length according to their point of origin in the apodeme. The muscles passing to the first pair of legs are also supported by the apodeme, which passes from the prothorax to the prosternum, and if this be dissected out it is seen to pass through some of the individual strands of the [illegible].

On the ventral surface of the thorax there is no muscle plate resembling that of the pediculi infesting man, but two transverse muscle bundles, passing, respectively, between the ventral borders of the coxae of the second and third pairs of legs, are present and correspond to the intercoxal muscles described by Müller. The anterior band consists of four strands, and in these are inserted the posterior arms of the apodeme of the prothorax

and prosternum. It lies just anterior to the stomach, below the esophagus, and is covered ventrally by the thoracic ganglia and many fat cells. The posterior band consists of two strands and passes across the ventral surface of the stomach. From each of the points of its insertion in the coxae of the third pair of legs, a muscle passes somewhat obliquely cephalad, and these muscles are inserted in the posterior arms of the apodeme where they enter the anterior transverse muscle band. In sections made through lice having the stomach filled with blood, the transverse muscle bands appear to be imbedded in the stomach, owing to its walls having become distended on either side of them.

The work of Landois and of Muller has made known the great difference in the longitudinal abdominal musculature of the two sexes of the man-infesting louse, and Nuttall (1917 a:296) has summarized this difference as follows:

	Dorsal abdominal muscles are present under segments	Ventral abdominal muscles are present under segments
In the male	2, 3, 4, 5, 6, 7, 8	2 + 3, 4, 5, 6
In the female	6, 7, 8	2, 3, 5, 6

In the hog louse no such difference is found. In both sexes a dorsal muscle extending the whole length of the abdomen is present. It consists of some eight muscle strands on either side of the median line. In segment 1 these strands converge to the point of their attachment to the posterior surface of the metathoracic apodeme, and posteriorly, in segments 8 and 9, the two halves of the plate diverge and the heart lies between them. The contraction of the muscle plate raises the posterior end of the abdomen. In both sexes the ventral muscle plate (Plate LIX, 4) begins in the anterior border of segment 2 and extends caudad to the posterior border of segment 6. The number of strands in each segment is apparently not arbitrary, and the following have been found most frequently:

	Number of strands in male	Number of strands in female
Segment 2,	12 central and 4 lateral	10 central and 4 lateral
Segment 3,	14	18
Segment 4,	14	16
Segment 5,	14	16
Segment 6,	14	16

In segment 2 the four lateral strands frequently appear as three, because the two outermost fuse almost immediately after leaving their attachment between segments 2 and 3. At their proximal end these lateral strands are attached to the lateral body wall a short distance cephalad of the anterior border of the pleurite of segment 3, and at their distal end, when looked at from their ventral aspect, the innermost strand and a part of the next innermost are seen to underlie the three outermost of the central strands. The dorsal and ventral muscle plates are composed of segmental muscles in which the attachment between those of the successive segments has become stronger than their attachment to the intersegmental folds of the body wall, so that the dorsal and ventral muscles can be dissected off as entire muscle plates.

While the two sexes bear a close resemblance in the longitudinal musculature of the abdomen, they show a marked contrast in the dorso-ventral musculature. In the male the digestive and reproductive organs occupy only the center of the abdomen, but in the female the ovaries occupy most of the lateral regions as well. In the male there is a powerful dorso-ventral musculature, which not only assists in respiration but plays an important part in the act of copulation. That part of each of segments 2 to 8 between the alimentary canal and the lateral body wall is filled with stout blocks of muscle, definite in number and arrangement for each segment (Plate LIX, 5). In segment 2 there are two blocks of muscle, in segments 3 and 4 eight blocks, in segments 5, 6, and 7 nine blocks, and in segment 8 eight blocks. The tracheae from the stigmata to the lateral trunk pass between these blocks of muscle, and between the muscle and the lateral body wall lie numerous fat cells. In segment 9, where the muscles controlling a part of the copulatory apparatus originate, there are no dorso-ventral blocks of muscle.

In the female there is a deep lateral indentation between the successive segments from 3 to 8, that between segments 6 and 7 being somewhat deeper than the others. Internally these indentations have the appearance of pillars or sections of the cuticula which divide the lateral parts of the successive segments into a series of small chambers. At the end of each cuticular pillar two bands of muscle are attached to the dorsal and ventral walls of the abdomen, and these curve close to the centrad wall of the pillar. In segments 4, 5, 6, 7, and 8, in the anterior half of the segment

there is a moderately stout band of muscle which is attached to the dorsal and ventral cuticula between and in line with the bases of the pillars. Within the lateral chamber of each of segments 3 to 8 there is a group of five slender muscle strands, and in segment 9 there are six larger strands. On the ventral surface these delicate strands are attached to the body wall just below the strongly chitinized pleurite, and from there they pass somewhat obliquely centrad and dorsad to the cuticula just within the central border of the chamber.

The leg muscles are similar in both sexes and show no unusual modifications except in those controlling the claw. Landois (1865 a:33 and 1865 b:495) studied in part the leg muscles of the man-infesting pediculi, and Muller (1915:14) has figured the muscles of the leg of a female clothes louse. As already said, Osborn (1904) described the musculature controlling the tarsus and claw of the hog louse. There are four muscles in each coxa, which originate in its articulation with the thorax and are inserted in its articulation with the trochanter. Within the latter are the flexor and extensor muscles of the femur, with their origin and insertion in its proximal and its distal articulation, respectively. The flexor muscle of the tibia is made up of a number of fibers which originate at intervals along the dorsal wall of the femur and come together in one tendon for their insertion in the ventral line of the articulation of the femur with the tibia. The extensor muscle is made up of two bundles of fibers originating in the articulation of the trochanter with the femur and in the proximal dorsal wall of the femur; it ends in two tendons which are inserted in the articulation of the femur with the tibia on the dorsal side of the leg. In the tibia there is one large muscle, made up of a number of closely set fibers which originate in the proximal posterior and ventral walls of the tibia. The muscle passes along the whole length of the segment, midway giving off a branch which is inserted in the base of the protractile disk. On entering the tarsus the muscle becomes a tendon which ends in a strongly chitinized process of a diameter somewhat greater than that of the tendon itself. It is inserted in the ventral wall of the tarsus under the base of the blunt process situated there, so that its anterior end lies just within the border of the claw and is attached to its ventral curve. The position and attachment of this muscle has been determined from the study of mounts of gross specimens and from numerous dissections of legs. It must be regarded as the extensor muscle of the claw, and the

branch going to the disk must be the retractor muscle of the disk. Osborn figured this large muscle lying in the tibia as inserted in the dorsal wall of the tarsus, and a continuation passing from there to the dorsal curve of the claw. He also figured a flexor muscle of the tarsus. Neither of these two conditions has been found in the present investigation, and the absence of flexor muscles of the tarsus and the claw may be explained on the following grounds: the tarsus becomes defined as a segment distinct from the tibia only after the final molt, and is then practically immovable, while the claw in its normal resting position is bent over with its tip touching the ventral anterior extension of the tibia, so that only an extensor muscle is necessary for its function. No mechanism for ejecting the protractile disk has been found, and, as Osborn suggested, this ejection may be accomplished by means of an elastic framework.

The foregoing account deals only with what may be called the skeletal muscles of the louse. The muscles controlling the various systems of the body are described later in their respective connections.

The histological structure of the muscle is best seen in the material fixed in Bouin's solution and stained with Mallory's anilin-blue connective-tissue stain, when all the cross-striations stand out with great clearness. All the muscles have a well-developed sarcolemma and are richly supplied with peripheral nuclei.

THE VASCULAR SYSTEM

In the writings of the early investigators of the Pediculidae, no real description of the dorsal vessel is to be found. Landois (1864 II), after many attempts, distinguished in freshly molted insects a slender tube originating in the region of the transverse tracheal band. He traced it cephalad to the middle of the abdomen, but could follow it no farther. Its pulsations were more rapid than those of the stomach. Mjoberg (1910:223) pointed out the similarity of the heart in the two groups which he studied, and drew attention to the lack of any thorough work in the Siphunculata (Anoplura). According to Schröder (1912:13:390), Provazek in 1905 described and figured the heart of *Haematopinus spinulosus* Burm., and this appears to be the first anatomical description of the heart of a siphunculatan. Müller (1915:27) has figured the heart of the clothes louse in gross and in sections, and has described in detail its anatomy and its pulsations in living specimens. Harrison (1916b:220)

again called attention to the similarity of the heart in Mallophaga and Siphunculata (Anoplura), and referred to Fulmek's (1905) work on Mallophaga, in which there is a short résumé of the literature of the heart, beginning with the work of Wedl (1855), who first distinguished in the dorsal vessel a posterior, specially contractile part — the true heart — and an anterior, more vessel-like part — the aorta.

In the hog louse the heart lies in the two posterior abdominal segments, between the halves of the dorsal muscle plate, and is attached to the dorsal wall on either side of the median line by two delicate septa. It is oblong-ovate, measuring approximately 0.38 millimeter in length and 0.075 millimeter in breadth, and has two lateral indentations on either side which give it a three-chambered appearance (Plate LIX, 6). Attached to the lateral and ventral surfaces are three pairs of wing muscles which pass directly laterad under the two halves of the dorsal muscle plate and are inserted in the lateral body wall toward the ventral surface. To the central wing muscles on either side is attached a group of six pericardial cells similar to those described by Fulmek (1905:620) in *Nirmus* sp. In gross dissections the ostia cannot be clearly seen, but sections show three pairs, lateral in position. Anteriorly the heart leads into the aorta, which lies free throughout most of its length in the body cavity and passes cephalad entering the head alongside the esophagus. Its width varies from 0.03 millimeter at the posterior end to 0.02 millimeter at the anterior end. In some few cases it seemed swollen to a bulb in the region of segments 6 and 5, but we did not find this to be a constant character.

The wall of the heart is very thin, and in section it is seen to be of uneven thickness (Plate LIX, 7). Its histological elements appear to be mostly muscular, and, while nuclei are visible, they resemble those of the sarcolemma rather than those of a true epithelium. Where the wall is slightly contracted, it has a false appearance of being toothed. Where the heart passes into the aorta there is a succession of six pairs of valve-like structures extending from opposite walls of the aorta into its lumen and almost meeting on the median line. Sections showed no definite structure that would reveal the true histological nature of these.

The blood is a colorless fluid and its cells can be seen singly and in groups scattered throughout the heart and the aorta. They are definite round cells with a well-defined central nucleus, and do not appear to be

numerous. Owing to the thickness of the cuticula it is impossible to watch the pulsations of the heart in living specimens, as was done by Landois (1864:11) and by Müller (1915:29) in the clothes louse.

The most successful preparations of the dorsal vessel have been obtained by first removing the dorsal cuticula of the whole abdomen and then the dorsal muscle plate. If the posterior attachment of the muscles of segment 9 be carefully loosened, the heart and its wing muscles will generally be found intact on the ventral surface of the muscle plate.

THE NERVOUS SYSTEM

Since the time of Swammerdam (1682, English trans. 1758:36), it has been known that lice possess three large thoracic ganglia and no abdominal ganglia, and that nerves pass backward from the metathoracic ganglion over the ventral stomach wall. It was not, however, until almost two hundred years later that a more detailed description of the central nervous system appeared, when Landois (1864:24) published his description of *Phthirius inguinalis*. He referred to Swammerdam as correctly describing three thoracic ganglia, and to Burmeister (1847) as incorrectly describing two in the Pediculidae. He figured the brain, the connectives, and the thoracic ganglia, but showed neither a sub-esophageal ganglion nor a sympathetic system. In his study of *Pediculus vestimenti*, published a year later (Landois, 1865 a:54), he found no noteworthy difference between the species. Brühl (1871:477) devoted his attention chiefly to the study of the peripheral ganglia, which he described as "Haar-Gehirne" and of which he counted approximately one hundred and fifty on each louse. Graber (1872:165) reviewed the work of Landois, and described the connectives between the brain and the thoracic ganglia as being at least four times the length given by Landois. On one occasion he found and figured a pear-shaped ganglion with two nerves passing backward from it. He thought it was the hitherto undescribed sub-esophageal ganglion, but, since it lay on the dorsal surface of the esophagus, he concluded that it must be a part of the visceral nervous system. Mjoberg (1910:222) did no work on the nervous system, but in a short note he mentioned the concentration of the ganglia in the thoracic region and the lack of any detailed work in both Siphunculata (Anoplura) and Mallophaga. A considerable advance has been made by Müller (1915:3–37) in his

description of the nervous system of the clothes louse, and he has called attention to the fact that, although in the mature louse the ganglia are concentrated in the thorax, in the embryo figured by Cholodkovsky (1903: 124) they extend some distance into the abdomen.

The central nervous system of the hog louse consists of five ganglia, their connectives, and commissures, and its approximate length from the anterior border of the brain to the posterior border of the metathoracic ganglion is 0.93 millimeter (Plate LIX, 8). The supra-esophageal ganglion lies in the posterior half of the head behind the level of the insertion of the antennae. It is a large, compact ganglion, deeply grooved anteriorly and surrounding the dorsal and lateral surfaces of the esophagus like a collar; its position is somewhat oblique, and the three segments of which it is composed are very closely fused. Its anterior lobes are joined on the ventral surface by the esophageal commissures, which can be easily seen in sections but are invariably broken in the process of gross dissection. These commissures were seen also by Muller (1915.34) in the clothes louse, and he suggested that they be named the "Commissura cerebri subpharyngealis." From the tritocerebron a pair of nerves pass out anteriorly and soon divide, one branch of each going to the frontal ganglion and the other to the labrum, where each subdivides into at least four branches terminating in large multinuclear sensory cells from which slender processes pass to the anterior wall of the head on either side of the rostellum. The ventral anterior part of the deutocerebron forms the olfactory lobes. In gross dissection these could not be distinguished, but they were found in series of longitudinal sections through the head, and from each a large nerve passes to the antennae. These nerves lie dorsad and somewhat laterad of the nerves from the tritocerebron. The optic lobes, also indistinguishable from the mass of the brain, send nerves out to the eyes, which are situated on prominences behind the antennae, are poorly developed, and are without pigment. The sub-esophageal ganglion is concealed anteriorly by the protocerebral lobes of the brain, and the esophageal connectives are so short as to be invisible unless the brain be teased. It is a heart-shaped ganglion, broadest anteriorly, and having a small indentation in which the esophagus rests. In sections, three pairs of nerves can be seen passing from it to the mouth parts.

From the apex of the sub-esophageal ganglion two closely apposed connectives pass backward along the median line to the prothoracic

ganglia. They measure approximately 0.22 millimeter in length. The thoracic ganglia are large and broad. Their approximate length is 0.38 millimeter and width 0.28 millimeter. They are closely fused, showing neither connectives nor commissures, but both in gross specimens and in sections it is evident that each ganglion has arisen through lateral fusion of two ganglia. They lie in the most anterior part of the thorax, and when the stomach is distended their position is oblique dorso-ventral rather than ventral. All three send out lateral nerves to the legs and the thorax, and the metathoracic ganglion sends in addition eight nerves to the abdomen, of which the two nearest the median line are the largest. These nerves pass backward to the ninth abdominal segment and give off in their course many slender branches to the visceral and reproductive organs.

The sympathetic system is well developed. The frontal ganglion is somewhat pear-shaped and lies some 0.03 millimeter in front of the brain, on the median line above the junction of the pumping pharynx with the true pharynx. Slightly laterad on either side of the ganglion a small nerve is given off anteriorly from the branches connecting the ganglion with the brain. The course of these nerves has not been seen, but they may connect the frontal ganglion with two smaller ganglia which are united to each other and lie on the median line above the anterior part of the buccal plate of Harrison (Plate LX, 1). Similar ganglia have been seen by Sikora (1916:28) in the clothes louse, and she has suggested that they are homologues of the prefrontal nerve plexus described in other insects. From the anterior end of the frontal ganglion a nerve passes forward on the median line, and from it numerous lateral branches are given off. From the posterior end of the frontal ganglion the recurrent nerve runs back, passing under the brain close to the dorsal surface of the esophagus and finally terminating in the thorax in a small ganglion situated above the entrance of the esophagus into the stomach. From this ganglion at least two slender nerves pass backward over the dorsal stomach wall

Both in gross dissections and in the study of serial sections, two sub-circular structures, of a diameter approximating 0.03 millimeter, have been found under the protocerebral lobes of the brain. They are made up entirely of ganglion cells, show no central substance, and stain more deeply than the surrounding tissues. In no case has any connection

been traced between them and the brain, but they are in close association with the tracheoles of the commissure passing under its posterior part. While a study of the texts of Berlese (1909:588) and Schröder (1912–13: 86) suggests that these bodies may be homologues of the "corpora allata" described by Carrière and Bürger in 1897, Heymons in 1899, Janet in 1899, and others, a knowledge of their development is essential for their correct interpretation. A short distance behind the brain and approximately above the esophageal ganglion, there has been seen in longitudinal sections of the head a ganglion in the course of the recurrent nerve, but no branches have been found issuing from it. This may be the hypocephalic or hypo-cerebral ganglion figured by Berlese (1909 596).

No attempt has been made to interpret a peripheral nervous system such as was described by Brühl (1871 477) in the pediculi infesting man, but if the nerve to the antennae be followed, it is seen to give off branches to the second and third segments which end directly under the cuticula in large multinuclear sensory cells similar to those at the termination of the labral nerves. In the terminal segment the nerve breaks up into branches corresponding in number to the blunt spinelike processes on the terminal sensory plate. Each branch terminates under its process as an oblong-ovate multinuclear sensory cell (Plate LIX, 9), but the actual connections between the cells and the processes have not been seen. Similar sensory cells have been seen in a few sections underlying the hairs of the abdomen.

THE STOMODAEUM, MOUTH PARTS, AND SALIVARY GLANDS

Writing of the clothes louse, Sikora (1916.22) says: "Es gibt kaum ein anderes Insekt, über dessen Anatomie so lange gestritten wurde, und über das so viele voneinander gänzlich abweichende Meinungen geaussert worden wären, wie die Laus." Most of the literature is the outcome of investigations of the man-infesting pediculi, but in some instances more or less detailed comparative studies have been made on the hog louse. With a few exceptions workers have confined themselves to the study of the mouth parts and their homologies, and this for two reasons: first, because in the middle of the last century a controversy was carried on as to whether lice possessed biting or sucking mouth parts, and secondly, because the systematic position of the group, long a matter of uncertainty, was thought to be dependent on the morphological

interpretation of the mouth parts. Owing to the specialized nature of the mouth parts and the lack of any ontogenetic proof of their homologies, various interpretations have been offered by investigators according to their views of the affinities of the group.

The early naturalists of the latter half of the seventeenth century attributed sucking mouth parts to lice, and based their opinions on the experimental feeding of captive lice on themselves. Nitzsch (1818:304) confirmed the observations of Swammerdam as to the presence of a bristle sheath (not the true sheath, but the proboscis), and put forward the hypothesis that the inner tube of suction consisted of several setae. His drawings of the structure were published, not with the text, but posthumously by Burmeister (1838). A year later Erichson (1839:377) stated that previous workers had erred in their descriptions, and that the louse possessed no hooks on the haustellum but did have a pair of strong, four-jointed palpi and very distinct mandibles. This statement led to Burmeister's (1847) paper upholding and confirming the opinions of Nitzsch, in which he gave an account of the structures in the hog louse. His work, though in the light of more recent investigations incomplete and in parts inaccurate, was a distinct addition to the knowledge of the subject. It was followed the next year by a contribution from Simon (1848:274), who, in his treatise on skin diseases, described his joint work with Erichson and corroborated Erichson's statements as to the presence of true palpi and mandibles and the absence of a sucking apparatus.

The controversy was finally settled in 1864, when Schjödte (1864, English trans. 1866:213) published the results of his investigations and his interpretations of the artifacts which had misled the supporters of the biting-mouth-parts theory. In the same year Landois (1864:3) described the mouth parts of Phthirius as corresponding very closely with Erichson's and Simon's descriptions of those of *Pediculus capitis* and *P.* [illegible], but when he published the results of his investigation of the clothes louse (Landois, 1865a:34) he stated that his first interpretation was wrong and that the mouth parts were of the sucking type. Burmeister (1871) described the mouth parts of the three species affecting man, and along with Schjödte considered the piercing mouth parts as having arisen through a modification of the mandibles and the maxillae, a view which, according to Enderlein (1905:631), originated in 1853 with Taschenberg, who regarded the mandibles as a tube made up of two halves and the

maxillae as the bristles lying within it. Graber (1872:138) distinguished in the mouth parts of Phthirius an upper lip, an under lip (proboscis), and a sucking tube formed possibly by the fusion of the mandibles and the maxillae and capable of protrusion from the proboscis, but he did not realize the true nature of the piercers and their sheath. He saw these structures extending far back in the ventral region of the head, and interpreted them as the retractor muscle of the proboscis.

The next two in the long succession of publications appeared at intervals of ten years, and both dealt, one entirely and the other in part, with species affecting domestic animals. Strobelt (1882, English trans. 1883:86) described very incompletely some of the structures surrounding the mouth openings of *Linognathus vituli (Haematopinus tenuirostris)* without seeing the real mouth parts, while Meinert (1891–92:58) used *Haematopinus suis* to illustrate his study of the mouth parts of *Pediculus humanus* and figured the different parts of the apparatus. Meinert called the whole structure the pharynx, distinguishing the anterior part of the stomodaeum proper as the epipharynx and the ventral sheath and piercers as the hypopharynx.

A third decade passed before another contribution appeared, and then Cholodkovsky (1903:120) attacked the subject from a different aspect. Realizing the uncertainty pervading all the earlier literature—most of which had appeared before the application of section-cutting to investigation methods—as well as the urgent need of embryological studies to supplement the early work of Melnikow (1869:153), Cholodkovsky not only studied mature species of Pediculus and Haematopinus, but also many mounts and serial sections of different stages of embryos of two of the species infesting man. The result led him to believe that mandibles and maxillae are present in the early stages of the development of the germ band but disappear entirely before the escape of the young insect from the egg, and that the piercer sheath and its apparatus are formed from the labium alone. Melnikow (1869:153) had emphasized the relationship between the Mallophaga and the Pediculidae, and considered both as a family of the Rhynchota. Cholodkovsky agreed with the first part of this statement, but thought the two groups should rather be classed with the Orthoptera (particularly with Pseudoneuroptera), or, preferably, should be placed in a separate order by themselves, for which he suggested the name Pseudorhynchota.

This suggestion was criticized by Enderlein (1904:121 and 1905:626), who, believed that these insects were hemipterous in their affinities, and consequently homologized the piercing apparatus with the maxillae, hypopharynx, and labium of the Rhynchota. His method of investigation was by gross dissection and by the study of cleared and mounted specimens. He used a number of related forms but gave the most detailed work to the interpretation of the hog louse. He compared the "mandibles" of the latter with those of the Corixidae, a proceeding which led to a discussion of the question by Handlirsch (1905:668), who emphasized the much clearer resemblance existing between the mandibles of the Siphunculata (Anoplura) and of different species of Mallophaga as figured by Snodgrass (1899). One outcome of the controversy between Cholodkovsky and Enderlein was the publication by Pawlowsky (1906:156) —a pupil of Cholodkovsky —of a résumé of the literature up to his time on the mouth parts of lice, and a description of the anatomy of the piercing and sucking apparatus of the Pediculidae.

Mjoberg (1910:203) made no study of the mouth parts but confined himself to a brief summary of the work of others, dealing at greatest length with Enderlein's work on the hog louse and his interpretation of the mandibles. Patton and Cragg (1913:531) gave an account of the mouth parts of *Pediculus vestimenti* "prepared, with the assistance of the above papers [of Enderlein and Pawlowsky], from sections and dissections." This account included also a description of the first part of the alimentary canal. The fact that the man-infesting pediculi are an etiological factor in the transmission of certain diseases has led to the publication within the last few years of three detailed papers on the anatomical structure of the anterior part of the alimentary canal and of the mouth parts proper. Those of Harrison (1916b) and Sikora (1916) appeared almost simultaneously, and that of Peacock (1918) some two years later. Owing to war conditions the work of Sikora was not available to the other two investigators, nor their work to her. Harrison and Peacock confined their investigations to the species affecting man, while Sikora introduced several species, among them the hog louse, to the purposes of comparative study.

The head of the hog louse is most strongly chitinized on the lateral regions, and the chitinization extends a little way beyond the borders of both dorsal and ventral surfaces. The remainder of the ventral surface is only weakly chitinized, and at the anterior end the integument is

capable of considerable wrinkling; while the dorsal surface is strengthened by three rigid transverse areas, one in the region of the clypeus, a second between the bases of the antennae, and a third above the anterior part of the brain. At rest the mouth opening is a longitudinal slit and is not visible from the dorsal surface. At the anterior border of the head on either side of the mouth opening are two strongly chitinized areas, which extend a little way onto the dorsal surface of the head but considerably farther onto the ventral surface, and on each of which are situated two pairs of bristles (Plate LX, 2–4). Sikora (1916, 13) found in the six species of lice she studied — *Pediculus vestimenti*, *Haematopinus suis* and *H. eurysternus*, *Polyplax spinulosus* (End.), *Haemodipsus ventricosus* End.), and *Trichodectes rituli* (End.) — a paired chitinous structure having the form and size of mandibles, situated between the upper and lower lips and apparently adapted for biting or rasping. In sections made through the anterior head region (Plate LX, 1), structures corresponding in part to this description have been found, but they are apparently only very weakly chitinized and are not covered by an underlip. Their inner border is slightly serrated and they appear to be attached by slender muscles to the process on the inner lateral wall of the head with which the basal part of the "mandibles" of Enderlein are continuous. Whether these structures could play any part in feeding is uncertain.

The haustellum

Projecting in front of the anterior border of the head on the median line is a small tubelike structure, the haustellum. It is convex on the dorsal surface and has an open longitudinal slit, the buccal slit, on the ventral surface (Plate LX, 2 and 3). Its approximate length is 0.05 millimeter and width 0.03 millimeter, and its chitin is continuous externally with that of the head and internally with that lining the food canal. In the interior of the haustellum are four pairs of double teeth arranged in two longitudinal parallel rows. They are present in both young and mature lice and are known as the buccal teeth. At the inner end the haustellum is connected by a fold of soft cuticula with the buccal plate.

The buccal plate

The buccal plate (Plate LX, 2 and 3) is a strongly chitinized structure identical in width at its anterior end with the haustellum and at its

posterior widest part measuring 0.08 millimeter across. It has the shape of a capital A in which the crossbar is a slight curve, convex toward the apex of the letter, and on the dorsal surface the space between this curve and the apex of the letter is solid. Its total length from the anterior edge to the posterior end of the arms is approximately 0.22 millimeter. Laterally it curves downward and centrad, but the opposite sides do not meet, so that on the ventral surface there is an open slit continuous with the buccal slit. The posterior arms of the buccal plate are fused with the lateral wall of the pumping pharynx.

The pumping pharynx

The pumping pharynx (Plate LX, 2 and 3) is strongly chitinized on the ventral and lateral surfaces and is capable of considerable dilatation on the dorsal surface. Its width at rest is 0.06 millimeter and the combined length of the buccal plate and the pumping pharynx is 0.5 millimeter. Its ventral surface extends forward to the posterior end of the ventral slit of the tubelike part of the buccal plate, and its dorsal surface is continuous with that of the buccal plate. Toward the posterior end there is a somewhat knoblike projection of the lateral walls, followed by a rather short backward prolongation of the more strongly chitinized part at the junction of the pumping pharynx with the true pharynx.

The pumping pharyngeal tube

From the anterior end of the pumping pharynx, two half tubes (Plate LX, 1 and 2) pass into the groove of the buccal plate but do not extend quite to its anterior end. Their ventral edges overlie each other, their dorsal ends lie apart, but so close under the buccal plate that a tube is formed through which blood is drawn during feeding. This tube has been called by Harrison (1916 b:209) the "buccal tube," by Sikora (1916: 26) the "Haustellumhalbrohre," and by Peacock (1918:101) the "pumping-pharyngeal tube." The true nature of the connection between this tube and the pumping pharynx can be followed only in sections, and is discussed later.

The pharynx

The pharynx (Plate LX, 1 and 2) was called by Enderlein (1904:127) the "larynx," and he described it as a chitinous band bent around on itself over the esophagus and never fused with the pharynx (pumping pharynx).

In cleared specimens he evidently saw only the anterior, strongly chitinized band of the pharynx. It is a somewhat cone-shaped structure having its widest diameter, which is approximately 0.15 millimeter, a little posterior to its transverse median line. In sections its ventral aspect is seen to lie almost level along the median longitudinal line of the head, and its dorsal surface passes obliquely toward the top of the head. Between its transverse median line and its part of greatest diameter is a more strongly chitinized region crossing the dorsal surface as a band and passing obliquely and posteriorly down the sides to the ventral surface, where the two bands run backward for a short distance, each lying somewhat laterad of the median line (Plate LX, 3). Behind the muscle insertions is a second region of strong chitinization, followed by a sphincter muscle, behind which the diameter lessens until it passes as the slender esophagus under the brain.

The œsophagus

The esophagus (Plate LX, 2 and 3) passes directly backward between the tritocerebral lobes of the brain, over the sub-esophageal ganglion, and into the thorax between the two main tracheal trunks. At the posterior end of the head the esophagus, the dorsal vessel, the tracheae, and the connectives between the sub-esophageal and thoracic ganglia, are inclosed by a wall of thin cuticula, which is continuous with and shows the same staining reactions as the cuticula separating the posterior end of the piercer sheath from the thorax. It is a structureless membrane (Plate LX, 5). At its posterior end the esophagus passes over the anterior part of the stomach lying in the thorax, and enters its dorsal surface under the tergite of the second abdominal segment. Its length from the posterior end of the true pharynx to its passage into the stomach is approximately 1.03 millimeters and its diameter 0.03 millimeter. In sections its wall is seen to consist of flattened epithelial cells lined by a thin chitinous intima, but no basement membrane can be distinguished. The usual muscle layers are present, but are so fine as to be distinguished only with considerable difficulty. At rest and empty, as it is seen in sections, the wall shows a number of small convolutions.

The "mandibles" of Enderlein

On either side of the pumping pharynx, where the posterior arms of the basal plate fuse with its lateral walls, lie two triangular chitinous

structures (Plate LX, 2 and 3) which Enderlein (1904:127) interpreted as "mandibles" and Sikora (1916:16) as "dreieckige Skelettstucke." Just anterior to the posterior dorsal margin of each is a groove, and at its lateral end articulates a rodlike structure which, according to Enderlein (1904:128), is the basal part of the mandibles and articulates anteriorly with the lateral wall of the head. Serial sections of the head show this basal part passing directly into the chitin of the wall, but show no articulation of the parts, a condition which has been described also by Sikora (1916:13–14). At their central angle these structures are attached to the sides of the pharynx by a structureless tissue, but it has not been found possible to determine the exact nature of the connection.

Musculature of the stomodaeum

During the act of feeding, the stomodaeum is moved forward by protractor muscles, and by the forward movement of the buccal plate the haustellum is protruded and the buccal teeth are everted (Plate LX, 4). There are two pairs of protractor muscles, a dorsal pair originating in the anterior wall of the head and having their insertion in the posterior arms of the buccal plate, and a ventral pair originating in the posterior lateral angles of the "mandibles" of Enderlein and having their insertion in the ventral surface of the knoblike processes at the posterior end of the pumping pharynx (Plate LX, 2). By the contraction of these two pairs of muscles the whole pharynx is moved forward.

There are three pairs of retractor muscles, two dorsal and one ventral. The former originate side by side on the dorsal wall of the head, lateral of the pharynx and just posterior to the muscles passing from the median line of the dorsum to the antennae. Both pairs of dorsal retractor muscles are of approximately the same dimension, and pass forward to end, the outer pair as long, slender tendons inserted in the lateral walls of the pumping pharynx in the margin of its fusion with the posterior arms of the buccal plate, and the inner pair, which lie close to the lateral wall of the pharynx, as much shorter tendons inserted in the dorsal surfaces of the posterior knoblike projections on the lateral walls of the pumping pharynx. The tendons of these muscles were recognized as such by Meinert (1891–92:Pl. I, fig. 3), and represent the "fulcrae" of Enderlein (1904:127). The ventral retractors originate in the latero-ventral wall of the head in the region of the anterior level of the brain,

They are somewhat smaller than the dorsal retractors, and are inserted as slender tendons in the ventral surface of the posterior knoblike projections of the lateral wall of the pumping pharynx.

In addition to protractor and retractor muscles, the pumping pharynx has six pairs of elevator muscles which originate in the dorsal wall of the head and are inserted in the flexible dorsal wall of the pumping pharynx. Four pairs of these muscles are slender. These originate somewhat laterad of the dorsal median line of the head, and pass rather obliquely centrad to their insertion in the median line of the pumping pharynx. The two remaining pairs of muscles, which are the second and fourth pairs in the succession from the anterior end, are much stouter. They originate in the dorso-lateral wall of the head and pass obliquely centrad to their insertion in the lateral edges of the two small chitinous plates imbedded in the roof of the pumping pharynx. Both their origin and insertion are distinctly laterad of those of the slender muscles. The frontal ganglion lies imbedded among these elevator muscles, and is protected laterally by the sixth pair, which, after their origin, pass rather obliquely backward for a short distance, until they meet the flexor muscles of the antennae, when they bend directly ventrad to their insertion in the posterior end of the pumping pharynx.

In the man-infesting louse, Harrison (1916b:213) describes two sphincter muscles, an anterior and a posterior, surrounding the pharynx; Sikora (1916:31) says there are many constrictors present; and Peacock (1918:105) describes an anterior, a medial, and a posterior sphincter. In this respect, as well as in the number and arrangement of the dilators, the pharynx of the hog louse is markedly different from that of the man-infesting louse. The whole structure is apparently covered with a layer of circular muscle, which varies considerably in thickness. Anteriorly, where the cuticula is only weakly chitinized, the muscle is well developed and surrounds the whole structure as a sphincter. Posteriorly, in the region of the first chitinized plate, the muscle is very thin except on the ventral surface, while in the region of the second chitinized plate it is thicker and on the median line sends off a number of strands which pass directly upward between the dilator muscles to the dorsal wall of the head. Before the pharynx passes into the esophagus the muscle layer assumes a moderate thickness throughout, and this part may be called the posterior sphincter. Only in its posterior

half is the wall of the pharynx capable of any dilatation, and there are inserted four muscles of which the two median are the largest. They originate in the dorsal wall of the head above the anterior lobes of the brain, and pass obliquely forward and downward to their point of insertion. Their contraction, while it may dilate the pharynx, would seem rather to draw it back to its resting position.

Between the eye prominences and the neck three bands of muscle originate in the lateral wall of the head. The median band extends farthest back and the ventral the next farthest, while the dorsal is the shortest. Just behind the antennae these bands unite in a common tendon which is inserted in the anterior lateral angles of the "mandibles" of Enderlein. In his first description of the mandibles (1904, 128–129) Enderlein did not see these tendons, but in his second paper (1905, 629–630) he describes and figures them as the tendons of the mandibular flexors. He also figures tendons passing forward from the posterior lateral angle of the mandibles to the anterior wall of the head, and calls them the tendons of the mandibular extensor. Sikora (1916: 16), however, describes these last as a uniformly thin strand passing from the ventral border of the triangular skeletal piece to the side of the underlip. In gross dissections the "mandibles" remain attached to the anterior wall of the head by this strand, but its true histological nature has not been determined, since it has not been identified in any of the series of sections made through the head. Enderlein found the "mandibles" well developed only in the hog louse, but considered that the finding of the muscle tendons removed every doubt as to their morphological interpretation. Sikora (1916: 13, 17), on the other hand, reserves the term "mandible" for the already-mentioned structure lying between the upper and lower lips and adapted for biting or rasping. She calls the "mandibles" of Enderlein "gewolbten Chitinplatten" or "dreieckige Skelettstucke," and denies the possibility of their being mandibles on the ground of their position back in the head and their separation by the pharynx. She suggests two functions for them, namely, to draw the pharynx forward and to transmit to the true mandibles the motor impulse of the muscles. Since the "mandibles" are attached to the lateral wall of the pumping pharynx and the buccal plate, the contraction of the tendon muscles would exert a backward pull on their anterior angle, and they, working as a lever, would serve to push forward the buccal plate and the pharynx, a function [illegible]

by the two pairs of protractor muscles. Sikora's second suggestion is based on the fact that she (1916:18) regards the basal part of the "mandibles" of Enderlein as the posterior articular processes of the true mandibles, which Enderlein (1905:637) in turn has interpreted as the ventral prolongations of the lateral sclerite. According to Enderlein these are pushed far under the scalelike labium and are covered by it ventrally. Sikora attributes the double function of opening the mandibles and moving forward the pharynx to the ventral protractor muscles, and their closing to the contraction of the tendon muscle. No constructive criticism of this interpretation is offered for the present, because it is believed that the final morphology of the parts can be determined only by embryological investigation.

The mouth parts

From the ventral surface of the stomodaeum at the junction of the buccal plate and pumping pharynx a diverticulum is given off. It passes backward under the alimentary canal to the extreme posterior end of the head, which is separated from the thorax by a thin, structureless, cuticular membrane, staining pink in hematoxylin and eosin preparations. Within this diverticulum lie the piercers and the salivary duct. The piercers (Plate LX, 7 and 8) consist of dorsal and ventral elements, and their total length is approximately 1.2 millimeters. The ventral element is made up of two parts, a dorsal and a ventral, which are very closely apposed to each other throughout the greater part of their length.

The sheath

The wall of the sheath is continuous with that of the stomodaeum and consists of somewhat flattened epithelial cells lined by a fine chitinous intima (Plate LXI, 7). On its inner surface next the coelom the sheath is also covered by a fine chitinous cuticula, the origin of which is discussed later. Its dorsal and lateral walls are of uniform thickness and appearance, while on the ventral wall there is imbedded a chitinous plate. This plate occupies approximately the posterior two-thirds of the floor of the sheath and is separated from the anterior third by a transverse suture. A similar condition has been described by Harrison (1916b:209) in the body louse. In this region of the plate there is a central groove in the

floor of the sheath. Posteriorly the diameter of the sheath decreases, until in the region of the rami of the piercers it surrounds them closely.

The piercers and the salivary duct

The piercers resemble long-handled two-pronged forks, having the prongs, which are 0.23 millimeter in length, situated posteriorly. They are long and slender, and lie free in the anterior part of the sheath, while their posterior forks are imbedded in tissue, completely filling the lumen so that sheath and piercers form a compact mass. This tissue extends forward among the piercers in two slender, pointed prolongations. A similar arrangement of tissue has been described by Sikora (1916:38) in the clothes louse. The dorsal element consists of two half tubes which in sections appear like two brackets having their contiguous edges fused (Plate LXI, 2). Posteriorly these become flattened, and after forking attain a width of 0.25 millimeter at their widest part, whence they narrow again and finally end in two ligament-like bands which come together at the point of their insertion in the posterior wall of the sheath. Anteriorly the two halves do not lie side by side, but are curved upward and toward each other so as to form a tube. The ventral aspect is made up of two parts, a dorsal and a ventral, which are closely apposed to each other but can be pulled apart without injury to either after being dissected out from the surrounding tissue. The posterior rami of the dorsal part are wider than those of the dorsal element of the piercers, and are somewhat different in shape (Plate LX, 6). They do not become flattened, and in sections appear subcircular. A small lateral process is given off from each shortly before they unite to form the piercer, which is a moderately heavily chitinized groove with more delicate edges spreading out flangelike over the edges of the ventral part of the piercer (Plate LXI, 1). The latter is also a canal-like structure (Plate LXI, 2), and its posterior rami are imbedded in the floor of the sac. Both parts of the ventral element of the piercers are bilobed at their proximal end. The lobes of the ventral half are somewhat wider apart than those of the dorsal, and both are finely serrated.

The salivary duct lies between the dorsal and ventral elements of the piercers, and at its posterior end is dilated in the form of a slender bulb which can be seen lying between the rami of the dorsal elements to the ventral surface of which the duct is attached through part of its length

by a strand of tissue. Anteriorly it appears to lie free between the elements, while just behind the haustellum it lies within the canal of the dorsal part of the ventral element. This duct was seen and figured by Stevenson (1905.13), but its function was not recognized until Harrison (1916b 209) carried out his investigation of the mouth parts.

When the piercers leave the sheath at the junction of the buccal plate with the pumping pharynx, they bend at an obtuse angle and pass forward in the groove of the buccal plate beneath the pumping pharyngeal tube to the mouth opening (Plate LXI, 1–4).

Musculature of the mouth parts

In the region of the rami the sheath is no longer a structure distinct from its contents, and both sheath and contents are controlled by one set of protractor muscles (Plate LX, 6). These originate as slender strands in the posterior end of the sheath, where the free ends of the rami are imbedded in its wall. They pass forward along the ventro-lateral borders of the sheath and are inserted in the lateral borders of the ventral plate (Plate LX, 6). The individual strands vary in length, so that, if they be detached from their origin and pulled away from the sheath, they resemble the extended dorsal fin of a fish. The longest strands extend to the anterior border of the plate. The contraction of these muscles bends back the ventral plate and telescopes the hinder part of the sheath into the front part, so that the piercers are pushed out of the head.

The retraction of the piercers and the sheath to their resting position is brought about by two sets of retractor muscles, a lateral and a posterior. The lateral retractors consist of two muscles originating in the wall of the head and inserted in the lateral wall of the sheath in the region of the anterior border of the ventral plate. The dorsal lateral retractor originates in the dorso-lateral posterior angle of the head and passes obliquely downward and forward between the bands of the tendon muscle and the brain to its insertion in the sheath. The ventral lateral retractor is considerably shorter than the dorsal, and originates in the latero-ventral wall of the head alongside of the ventral retractor of the pharynx, whence it passes forward to its insertion in the sheath (Plate LX, 6). The posterior retractors are two large muscles lying on either side of the end of the sheath almost in the neck, two muscles lying under its ventral surface, and two lying on its dorsal surface. Each of the first has a

double origin, one branch originating in the dorsal wall of the head and the other in the chitinous cuticula between the head and the thorax. After the fusion of the two branches each muscle passes ventrad and slightly forward to the level of the floor of the sheath, where they bend at a rather sharp angle and pass a little way backward to their insertion in the floor of the sheath under the anterior ends of the rami (Plate LX, 6). The ventral muscles are two stout strands originating in the ventral wall of the neck and passing forward under the sheath almost to the angle of its posterior retractors, when they bend sharply back on themselves. Each muscle almost immediately divides into two slender strands, which are inserted in the posterior ends of the rami of the elements of the ventral piercer. They are the retractors of the ventral element of the piercers. The dorsal muscles lie on the dorso-lateral wall of the sheath and are the retractors of the dorsal element of the piercers. They originate in the posterior chitinous cuticula between the head and the thorax, and lie doubled on themselves just as do the retractors of the ventral element of the piercers. They are inserted in the posterior ends of the rami of the dorsal element of the piercers. The lateral posterior retractors control the sheath and the piercers, while the dorsal and ventral posterior retractors control the movements of the separate elements of the piercers. The contraction of the lateral retractors of the sheath brings its anterior part to a resting position, and the simultaneous contraction of the posterior retractors begins the withdrawal of the mouth parts from the wound. They come to their final resting position through the relaxation of the protractor muscles and the consequent straightening, through its own elasticity, of the plate imbedded in the floor of the sheath.

The true relationship between the pharynx and the sheath and mouth parts can be fully understood only if the study of serial sections supplement that of gross dissections and mounts *in toto*. In a section through the head at the anterior level of the attachment of the basal piece of the "mandibles" of Enderlein to the lateral wall of the head, the two halves of the dorsal piercer are seen lying tubelike close under the dorsal wall of the buccal plate and are here more strongly chitinized than elsewhere. Beneath it lies the ventral element of the piercers, with the salivary duct in its canal (Plate LXI, 1). The pumping pharyngeal tube does not reach this far forward when in its resting position. From the ventral wall of the buccal plate two outgrowths are continued ventrad as chitinous

cuticula on either side of the mouth parts, below which they pass closer to each other for a short distance before turning at right angles and passing to the lateral walls of the head. At the anterior level of the "mandibles" (Plate LXI, 2) the buccal plate is somewhat more tubelike, but it still continues ventrad as a delicate cuticula alongside the mouth parts. This prolongation appears now to be a continuation of the dorsal and ventral surfaces of the plate, while in succeeding sections it comes to be a continuation of the dorsal ends of the pumping pharyngeal tube, the anterior ends of which are now seen lying between the buccal plate and the dorsal element of the piercers. In this anterior region a band of tissue crosses the head transversely above the stomodaeum and appears to be attached at either side to the lateral wall of the head just dorsad of the basal part of the "mandibles" of Enderlein. It is very similar to epithelial tissue, and each cell has a definite nucleus lying near its base. The cells attain a considerable length, particularly on either side of the stomodaeum, and their dorsal surface is attached to a well-defined basement membrane. In sections stained with iron hematoxylin they closely resemble secreting cells. At the level of the articulation of the basal part of the "mandibles" of Enderlein with the triangular part, this band of tissue rests on the top of the buccal plate, and at its most posterior part it appears to form an attachment between the buccal plate and the lateral wall of the head. The buccal plate gradually becomes flat and there is a marked increase in the thickness and rigidity of the dorsal wall of the head. Also the shape of the buccal cavity changes, marking the beginning of the ventral wall of the diverticulum, but the mouth parts are still lying under the pumping pharyngeal tube. As the chitinous intima of the buccal cavity passes dorsad, it curves around into the lateral edges of the dorsal element of the piercers, and at this point shows stronger chitinization, afterward continuing as a fine cuticula to the ventral ends of the halves of the pumping pharyngeal tube. The dorsal ends of these half tubes are also continued as a fine cuticula, which passes downward to surround the ventral part of the buccal cavity. Between these two chitinous layers is a layer of epithelial tissue which broadens considerably on either side of the mouth parts and there appears to contain some muscular elements (Plate XLI, 3). Immediately behind the section shown in Plate XLI, 3, the buccal plate divides into two arms united by a thin cuticula which forms the roof of the pumping pharynx and which, as it passes backward,

is raised in a ridge along the dorsal median line (Plate LXI, 4). The cuticular strands coming from the now more widely separated dorsal ends of the halves of the pumping pharyngeal tube are at first strongly chitinized and pass laterad to the edges of the arms of the buccal plate, where they turn ventrad and surround the sheath as a basement membrane to its epithelium. The inner cuticula of the sheath is continued upward to the ventral ends of the pumping pharyngeal tube as shown in Plate LXI, 3, but the strong chitinization in the region of the dorsal piercers extends farther dorsad, and the points passing around their lateral edges are less curved downward. The gradual movement centrad and ultimate fusion of these points cuts off the piercers from the pumping pharyngeal tube. At the same time the strong chitinization continues dorsad until it fuses with the ventral ends of the pumping pharyngeal tube, which gradually move apart. In this way the pumping pharynx is formed, which, at its anterior end, has the ventral surface much narrower than the dorsal (Plate LXI, 5). The cuticula coming from the dorsal ends of the pumping pharyngeal tube is thick and strong, and fuses with the lateral edges of the arms of the buccal plate, which are here elevated knoblike and form a firm base for the insertion of the dorsal protractor muscles (Plate LXI, 4). From their lateral edges the thin cuticular layer still extends downward to surround the epithelium of the sheath. The floor of the pumping pharynx gradually broadens and assumes a rounded shape (Plate LXI, 6). In only two areas — those of the insertion of the two large pairs of dilator muscles — is there any strong chitinization of the dorsal wall of the pumping pharynx. Just behind the anterior area and after the floor has become rounded, the pumping pharynx and the diverticulum become entirely separated from each other, and a short distance behind this separation the chitinization of the ventral wall becomes stronger and that of the lateral walls less strong (Plate LXI, 7). The dorsal wall only is capable of dilation, and in the figures is seen in a resting condition. At the level of the antennae the ventral surface narrows somewhat and a stronger chitinization is evident throughout the structure as it passes into the pharynx. Also at the level of the antennae there appears the anterior part of the plate imbedded in the floor of the sheath, which becomes chitinized and bent to form a central furrow. The circular muscle of the pharynx is well developed and surrounds the anterior part as a plumeter (Plate LXI, 8), but in no case has a transverse section of the pharynx

appeared like a cross as it is figured in the man-infesting louse by the different investigators. The tissue of the pharynx wall is in parts very much developed, but its precise histological nature has not been determined. Neither in appearance nor in staining reaction does it correspond to a simple epithelium. Where the wall of the pharynx is strongly chitinized, both the muscle and the epithelium are thin (Plate LXI, 9), but in the region between the second area of chitinization and the transition to the slender esophagus the wall is so thick that the lumen is reduced at rest almost to a slender transverse slit (Plate LXI, 1).

The salivary glands

Since the time of Landois (1864:9) it has been known that lice possess two pairs of salivary glands situated in the thorax. It was Pawlowsky (1906:199–200), however, who first described the glands opening into the piercer sheath, and his name has been given to these glands by subsequent workers. Still more recently a fourth gland, situated between the rami of the piercers, has been described.

Pawlowsky's glands are simple tubular glands lying on either side of the piercer sheath, into which they open through wide conduits at the level of the eyes (Plate LXII, 1). They have at this point a depth of 0.1 millimeter and a width of 0.05 millimeter, while their length is approximately 0.33 millimeter. They rest on the tendon of the dorsal lateral retractor muscle of the piercer sheath, and this causes an oblique indentation in their posterior ventral surface. They have a lining of epithelial cells which are not clearly defined from one another and which show the usual reactions to stains. Pawlowsky (1906:200) suggests that their secretion may serve to irritate the wound or to lubricate the piercing organs, but Harrison (1916b:217) has seen no sign of glandular activity and suggests that they are functionless. No secretion has been found in the lumina of the glands in any of the sections studied, but in a rather oblique longitudinal section there is some appearance of activity of the cells. This, however, may be due to the fact that the section is rather close to the lateral wall of the gland (Plate LXII, 2).

Between the rami of the piercers lies an unpaired gland (Plate LX, 5 and 6), which was first seen by Sikora (1916:54) in *Pediculus vestimenti* and was called by her the "Stacheldrüse." It is somewhat wedge-shaped, being broadest at the anterior end, is clothed with cylindrical

epithelium, and appears to be continuous with the posterior end of the chitinous bulb which marks the termination of the salivary duct

The two pairs of thoracic salivary glands lie closely apposed to either side of the anterior end of the stomach, and the long, horseshoe-shaped gland is folded around the oblong-ovate gland in a characteristic manner (Plate LXII, 3). In the man-infesting pediculi the glands are described as "kidney-shaped" and "horseshoe-shaped," and their position in the thorax has been variously figured by a number of authors but the smaller one has never been shown surrounded by the larger. Strobelt (1882, English trans. 1883:89) described the glands of *Linognathus vituli* (*Haematopinus tenuirostris*) as "elongated" and "globular," and thought that the efferent duct of the former was situated at one end of the gland and that the horseshoe appearance was due entirely to the position of the gland at rest. The length of the horseshoe-shaped gland (Plate LXII, 4) is approximately 0.66 millimeter and the width of the arms 0.33 millimeter. The length of the oblong-ovate gland (Plate LXII, 5) is 0.12 millimeter and its width 0.05 millimeter. The large cells of the epithelial lining shine through the outer membrane of the gland, and at the exit of the duct the transition from these to the small cells lining the duct can be seen even in gross specimens (Plate LXII, 6). In sections the epithelial cells are seen to be considerably larger than those of Pawlowsky's glands, and the nucleus, with its dark-staining nucleolus, lies rather toward the base of the cell. There is a distinct though small lumen within each gland. The efferent ducts of the two glands pass cephalad without uniting. In gross dissection they have been followed as far as their entrance to the head, but their union with the salivary duct lying between the dorsal and ventral elements of the piercers has not been seen. In his description of dissections prepared by Mr. Bacot, Entomologist to the Lister Institute, and the late Major Sidney Rowland, of the Royal Army Medical Corps, Martin (1913:85) says the four salivary ducts open into the base of the piercer sheath; while Harrison (1916b:209) has not succeeded in tracing definite connections between the salivary duct of the mouth parts and the ducts of the glands. Sikora (1916:50) describes the ducts as passing into the head alongside the esophagus as far as the posterior end of the sub-esophageal ganglion, where they turn back, and through a ventro-caudal bend reach the end of the piercer sheath. In *Pediculus vestimenti* she figures the two ducts of each side uniting

in a common duct for a short distance before entering the middle of the dorsal surface of the piercer sheath by a common opening, while in *Haematopinus eurysternus* she describes them as running separately to the opening into the salivary duct of the mouth parts. Peacock (1918: 115) refers briefly to Martin, and to a dissection made by Mr. Lloyd, Chief Entomologist to N. Rhodesia, as demonstrating that the four salivary ducts open into the bulbous structure at the posterior end of the chitinous salivary tube.

Of these interpretations that of Sikora is probably the most accurate, because it alone describes an arrangement of the ducts which allows of their being drawn forward by the mouth parts during feeding without danger of their rupture.

Patton and Cragg (1913:559) describe a small collection of round cells surrounding the esophagus and constant in position, which differ from the cells of the fat body in their more glistening appearance. They distinguished no duct with certainty, though in some dissections a fine filament, which may have been a duct, was seen passing upward with the salivary duct. Muller (1915) discusses these cells in connection with the fat body, but remarks that up to that time no fat has been demonstrated in them. Harrison (1916 b:220) says that in the Siphunculata (Anoplura), groups of specialized binucleate cells, richly tracheated, lie about the ducts of the salivary glands, at the base of the esophagus. Sikora (1916: 57–58) gives a detailed account of the structure and appearance of these cells, which she calls "grosszellige Drüsen," in *Pediculus vestimenti*, and mentions their presence in the other species investigated. She considers them as quite distinct from the fat cells and suggests that they withdraw some constituent from the body fluid and store it or act on it in some way before returning it to the body fluid.

In the hog louse there is a cluster of small, subcircular cells, arranged like a pair of wings, lying above the base of the esophagus. Between these cells and the esophagus pass cephalad the dorsal vessel and the ducts of the salivary glands. On dissection each half of the cluster is found to consist, on the average, of forty small cells united by a network of very fine tracheoles. The two median posterior cells, which are somewhat larger than the others and pear-shaped, lie side by side on the end of the esophagus with their pointed ends caudad, and from each of them a slender tracheole passes to the surrounding network of the fat cells

scattered on the dorsal anterior region of the stomach wall. We have found only two nuclei in any one of these cells, while four or five may be present in each fat cell. Recently Nuttall and Keilin (1921:184) have published the results of their investigation of these cells. By the intracoelomic injection of ammonia-carmine, they have demonstrated that the cells in question have, in Pediculus, an excretory-accumulatory function, and so they have named them *peri-esophageal nephrocytes*.

THE ALIMENTARY CANAL AND ITS APPENDAGES

The stomach of the hog louse (Plate LXII, 7) is a simple tubular structure measuring approximately 1.98 millimeters in length. It consists of a wider anterior part 1.38 millimeters long with a diameter of 0.62 millimeter, and a more slender posterior part 0.6 millimeter long with a diameter of 0.2 millimeter, and extends from the region of the mesothorax to that of the sixth and seventh abdominal segments, where it bends cephalad on itself for a short distance, receiving the malpighian tubes and passing into the intestine when it again turns caudad.

The stomach of the adult hog louse differs from that of the man-infesting pediculi in two respects: its anterior end is not divided into two blind pockets, and it does not possess a "Magenscheibe." Strobelt (1882, English trans. 1883:90) found no "Magenscheibe" in *Linognathus vituli* (*Haematopinus tenuirostris*), while Sikora (1916:62) found one in *Polyplax* (*Haematopinus*) *spinulosus* End. but not in *Haematopinus* (*Haematopinus*) *ventricosus* End. Sikora describes as present in young specimens of *Haematopinus suis* a refractive whitish body on the dorsal surface of the abdomen, which in sections shows a structure similar to that of the "Magenscheibe" of man-infesting lice. In the present investigation no such structure has been seen, but the majority of the specimens sectioned have been mature lice, and the structure, as Sikora's work suggests, may be present only in the immature stages.

That part of the digestive tract lying in the thorax anterior to the entrance of the esophagus differs markedly in its structure from the true digestive mesenteron. That it is to be considered as a terminal enlargement of the esophagus, comparable to the crop of certain insects, is suggested by a number of facts. In gross specimens the nature of the wall does not resemble that of the true mesenteron, because the circular fibers still lie outermost. At its distal end, just behind the entrance

of the esophagus the circular muscles become emphasized as a narrow band and the longitudinal fibers pass out from under them, forming, on the surface of the true stomach, with the underlying circular muscles an open-meshed network. A study of sections has revealed no trace f an esophageal valve, either where the slender esophagus passes into he enlarged part or where the abrupt transition to a digestive epithelium kes place, and the structure of the wall is identical in both slender and nlarged parts. A similar abrupt transition from the esophagus to the id-intestine without the intervention of a valve or a sphincter has been escribed in the bedbug, by Cragg (1915 709). It consists of a delicate uscular coat and a layer of much-flattened epithelial cells lined by a ne chitinous intima. In the region of the above-mentioned circular uscle band there is an abrupt transition to the digestive part of the omach, which is lined with a layer of secretory epithelial cells. In lice issected some hours after feeding, the thoracic enlargement is frequently ound empty; while in the anterior part of the true mesenteron there is considerable volume of blood, and if a smear be made from the contents f such a stomach a large number of intact corpuscles are found. Also, here digestion is taking place the active epithelial cells shine through he stomach wall as light spots among the blood, a condition never seen n the wall of the anterior dilatation.

At the junction of the stomach and the intestine, four malpighian ubes are given off. They measure approximately 6.3 millimeters in ength and 0.25 millimeter in diameter, and are about two and a quarter imes as long as the combined length of the stomach and intestine. They irst pass backward along the sides of the intestine, and then forward o the anterior end of the abdomen, where they turn again caudad ter- minating finally in the region of the last two abdominal segments. In structure they show no unusual features, and in no sections have secondary invaginations of their lumina been seen, such as are figured by Sikora (1916 67, Pl. III, figs. 14, 15) in *Pediculus vestimenti*.

Posterior to the malpighian tubes lies the small intestine. It has an approximate length of 0.43 millimeter and diameter of 0.2 millimeter. When empty its epithelium, which is much more slender than that of the mesenteron and is covered with a delicate intima, lies in six longitudinal folds. Three muscle layers are present, but are not readily distinguished

since the longitudinal fibers are gathered in six strands. There is no valve between the stomach and the small intestine.

Between the small and large intestines is a region, measuring 0.25 millimeter in diameter, which is characterized by the presence of six whitish, oblong-ovate plates imbedded in its wall (Plate LXII, 7). These plates, which in sections (Plate LXII, 8) are seen to extend a considerable distance into the lumen of the intestine, are surrounded by a large number of tracheae. They have no definite cell structure, their content is granular with nuclei scattered throughout, and in some sections irregular clefts are present which are evidently not due to mechanical rupture and may be definite lumina. No ducts opening into the intestine have been seen. With hematoxylin and eosin the groundwork stains an uneven pink, and with iron hematoxylin a light grayish brown. Whether these plates are modified glands is uncertain. Their inner surface is lined with a well-defined intima, and at either end a definite epithelium is represented by a few cells in the clefts between the plates, but in the middle of the region (Plate LXII, 8) no such cells are to be found. The inner layer of circular muscle is present, and the longitudinal muscle consists of six bands each made up of six or seven fibers lying in the indentations between the plates, but no outer circular layer has been seen. Sikora (1916, 67-68) calls these plates the "Enddarmdruse," and objects to the use of the name "rectal glands" on the ground that in the louse these plates have no connection with the rectum. Her figures of their structure in *Pediculus vestimenti* represent them as much more glandlike than they appear to be in *Haematopinus suis*. Toward the posterior end the cuticula increases considerably in thickness and the plates are succeeded by a well-defined epithelium. The longitudinal muscle fibers are lost sight of among the large circular fibers surrounding the rectum (Plate XLII, 9). This is a short, straight tube leading direct to the anal opening and measuring only 0.18 millimeter in length and 0.08 millimeter in diameter. Its wall lies in six folds, and it is lined by a thick cuticula which is not very strongly chitinized and stains a clear blue with Mallory's connective-tissue stain after fixation in picro-aceto-formol.

FEEDING AND DIGESTION

In experimental feeding, when a louse is placed on the arm it crawls around and appears to test the surface with the antennae and the sensitive

areas in front of the head. When the spot for feeding has been selected, the contraction of the dorsal and ventral protractor muscles, assisted perhaps by the contraction of the tendon muscles in the side of the head, moves forward the buccal plate and the pharynx, bringing the former with the inclosed pumping pharyngeal tube in contact with the skin. At the same time the haustellum is automatically pushed out, so everting the buccal teeth, which anchor the head to the skin of the host; and the sheath and piercers must also be carried forward, since the cuticula of the sheath is continuous with that of the buccal cavity. Immediately following the contraction of the protractors of the pharynx, the protractors of the sheath and the piercers contract and telescope the hinder part of the sheath into the front part, carrying with it the piercers and the salivary duct, which are inserted into the skin of the host. Salivary secretion passes into the wound, and probably contains an anti-coagulin similar to that demonstrated by Nuttall (1917c: 74) in the saliva of the man-infesting louse. The closing of the anterior sphincter of the pharynx causes a negative pressure in the pumping pharynx, the dorsal surface of which is meantime raised by the contraction of the dilator muscles, and the blood flows through the canal of the dorsal piercers to the pumping pharyngeal tube and so to the pumping pharynx. When the latter is filled with blood, the simultaneous relaxing of the interior sphincter of the pharynx and of the dilator muscles of the pumping pharynx drives the blood into the pharynx, whence it passes to the esophagus on the relaxation of the posterior sphincter. From the esophagus the blood is carried by peristalsis to the rest of the alimentary tract. The process can best be seen in newly molted specimens, and is so rapid that the muscles either act simultaneously or in very rapid succession. At the close of feeding, the whole structure is brought to its resting position by the contraction of the retractor muscles and the relaxing of the protractors, while the elasticity of the plate imbedded in the floor of its posterior region gives the final impetus to the piercers and the sheath.

The wall of the mid-intestine consists of the usual four layers, a delicate epithelium resting on a basement membrane and surrounded by inner circular and outer longitudinal muscles which are arranged in a very loose network comparable to that described by Cragg (1915:712) in the bedbug. The epithelium of the stomach is similar throughout, no definite areas being adapted respectively for secretion and absorption,

and in accordance with the mode of life of the insect it appears to be always in a state of activity. In the study of the epithelium many series of sections of the alimentary canal have been made, at intervals of from half an hour and one hour after the time of feeding up to twelve hours, by which time the stomach in captive specimens appeared to be empty of blood. Sections have also been made of lice starved to the point of death.

The epithelial cells vary in outline according to their state of activity. In the resting stage (Plate LXIII, 1) they are flattened and extend farthest into the lumen in the region of their nuclei. During absorption the individual cells expand until they appear cuboidal, and during secretion the free ends of the cells, where the ball of secretion accumulates, become subcircular. These secreting cells show great variation in the degree to which they extend into the lumen. They may remain attached to the basement membrane by a broad base, or they may be greatly attenuated and apparently attached to the membrane by a very narrow base, and in sections blood is seen extending between the individual cells (Plate LXIII, 1). In no case has a definite cell wall been found between any two cells, and the whole appearance suggests a syncytium; but further proof would be necessary before the acceptance of this view. Each cell has a large oval nucleus with a subcentral nucleolus surrounded by irregularly scattered chromatin granules. There is considerable variation in the position of the nucleus in the cell, and this, in addition to the irregularity of the cells, gives the effect of a several-layered epithelium (Plate XLIII, 1 and 2). In most cases the nucleus is seen lying in the cytoplasm immediately behind or to one side of the secretion products, and on their excretion remains intact, but in a few cases the nucleus has been seen to be carried along with the secretion (Plate LXIII, 2). In the latter case the death of the cell must follow, and the question of its replacement arises. In many insects a regular destruction of the epithelium takes place and new cells are formed from regenerative centers, or nidi; but no such structures are present in the hog louse, nor has Sikora (1916:65) found them in *Pediculus vestimenti*. Nuclear division has not been seen taking place in the epithelium, but just within the basement membrane at the base of and between some of the epithelial cells lie single, very small nuclei, each hardly more than a nucleolus, definitely surrounded by a small amount of protoplasm; and these may be the source of the new epithelial cells. A similar condition was described by Van Gehuchten

(1890:246) in the larva of *Ptychoptera contaminata*. The epithelial cells are bounded on their free edges by a border, which appears in most cases to be definitely striated.

Taken from its host and confined without food, the hog louse is a short-lived insect, and starved specimens invariably died in from twenty-eight to thirty hours after their last feeding. In lice killed, respectively, seventeen and twenty-four hours after feeding, and sectioned, the stomach was found empty of food, its walls contracted, and the majority of the cells swollen with secretion while in some cases the border of the cell was ruptured and the ball of secretion had escaped into the lumen. This would suggest that hunger stimulates the activity of the secreting cells, and also the liberation of their products into the lumen.

From a louse fed two hours previously, the stomach was dissected out in physiological salt solution and a part of the wall teased. Microscopic examination revealed the presence within the cells of two types of granules, f which the more numerous were fine, irregular-elongated, and dark, and he less numerous were coarse, round, and refractive. A 2-per-cent olution of osmic acid was then introduced under the cover glass, and the oarse granules turned black, showing them to be either lipoid or proteid, hile the fine ones probably represented secreting granules. A series f twelve lice were killed with chloroform at intervals of one hour and the tomachs immediately dissected out in a mixture of equal parts of 2-per-ent osmic acid and salt solution and fixed in Flemming's weak solution or twenty-four hours. After sectioning, some were mounted unstained nd others were stained with safranin. Absorption evidently began lmost immediately, for at the end of one hour a few deep black granules were found just beneath the border of the cells of the anterior region of he stomach. As the series was ascended, the black granules increased greatly in number and in size. The largest lay just under the border f the cell, and their size was in inverse ratio to the degree of penetration within the cell. In the first six of the series a definite increasing absorption ould be traced in the bulk of the cells lining the wide section of the tomach, and this absorption was going on even in cells forming secretion. n the latter the black granules lay in a circle outside the zone of secretion, nd were never seen to come in contact with it even in the few cases in which the border had given way and the secretion was in process of being xcreted In the louse killed at seven hours, absorption was proceeding,

not in the anterior, but toward the posterior, half of the stomach, in the region of the bend cephalad; and in the last numbers of the series it was found throughout the whole slender part of the stomach.

In the cells containing the greatest number of granules, some were seen resting on the basement membrane and a few appeared to be lying among the muscle fibers outside the membrane, but sufficient evidence to prove that they had passed through the membrane unchanged is wanting. Whatever may have been the fate of these granules, they disappeared from the cells, leaving in their places numerous vacuoles among which the first traces of secretion were seen. The secretion accumulated in the form of a compact mass, resembling a ball of thread, whose surface layer takes a deep stain while the axis remains almost clear. This ball pressed against the free ental border of the cell, pushing it into the lumen and finally rupturing it.

The above experiments show that absorption and secretion are carried on by the same cells. In every section some cells, evidently in a resting stage, are seen, but it is not clear whether the cells pass through this stage after each secretion or at longer intervals. The formation of the secretion appears to begin at the close of absorption, and, as the study of the starved lice suggested, its excretion is stimulated by hunger, so that it is already present in the stomach when the blood is ingested. No attempt has been made to investigate the exact nature of the granules or the changes they may undergo, as this would necessitate a long series of experiments with various reagents, such as were carried out first by Fischer (1899) and later by Murlin (1902).

If lice be fed as in the previous experiment, and blood smears be made from the stomach contents at intervals of one hour and stained with Wright's stain, the gradual action of the epithelial secretion on the blood can be followed. Within one hour after feeding, the red cells become vacuolated and fat globules appear, but the leucocytes and the platelets are evidently not affected. The changes in the red cells continue until only an amorphous mass remains, which, in sections stained with hematoxylin and eosin, can be recognized as a mass of brownish granules. No blood platelets have been seen in any but one-hour smears. At two hours the nuclei of the leucocytes are intact but their cytoplasm has been attacked; there is a gradual change in its staining reaction, and after three hours it takes the basic stain, appears light blue, and can be distinguished

from the background only with considerable difficulty. At six hours the nuclei of the leucocytes show the first signs of disintegration, while at eight hours the whole has an amorphous appearance and the hemoglobin is disappearing.

In accordance with their parasitic habit, hog lice probably draw blood from their host at frequent intervals and in small quantities; so that in any one specimen taken at random and fixed and sectioned, all stages of digestive activity will probably be found in the length of the mid-intestine. Those fed to repletion in captivity showed absorption taking place, as it were, in a gradual succession throughout the canal; and even in these cases, not only have one or more cells in a state of active secretion been found scattered among the absorbing cells, but absorption and secretion have been seen taking place at one time in the same cell.

THE FAT BODY

In both larva and adult the hog louse is richly supplied with fat cells arranged in a more or less definite plan. In the head they lie along the lateral regions among the muscles and are most numerous toward the ventral surface. There are also two small clusters dorsad of the sub-esophageal ganglion just behind the brain. On the dorsal surface of the thorax a cluster of fat cells lies above the occipital apodeme, while on the ventral surface, between the ganglia and the hypodermis, lie four compact, grape-like clusters which extend laterad to the coxae. In the abdomen, with the exception of three clusters on the dorsal surface in the region of segments 5 and 6 the fat cells are not arranged in compact groups but are more widely spread in dorsal and ventral peripheral layers. They are more numerous among the lateral abdominal muscles than among the viscera, particularly in the female. In the male these lateral cells are crowded between the blocks of muscle and the body wall in the neighborhood of the spiracles.

In gross dissection the fat cells can be removed in clusters held together by a rich network of tracheae. They are large, subcircular cells whose wall is a transparent membrane through which the granular content is clearly seen. In sections (Plate LXII, 10) the cells are seen to contain a variable number of nuclei, each with an oblong-ovate nucleolus surrounded by a clear zone in which are scattered chromatin granules of varying

sizes, the largest being peripheral in position. Both in cells stained with hematoxylin and eosin and in those stained with iron hematoxylin, the groundwork appears to be alveolar with many dark-staining granules adhering to the walls of the alveoli. When they are stained with iron hematoxylin and the differentiation with the iron-alum solution is not carried far, it is impossible to distinguish the fat from the other granules; but if the destaining is carried further than is customary, the fat retains its black color, while the other granules become a grayish brown.

In living specimens the distribution of the fat body is clearly seen shining through the integument, and in mature specimens there may be seen in the abdomen many green cells scattered among the white fat cells. In his description of the fat body of Phthirius, Landois (1864:11) mentioned emerald green cells which stood out with greatest clearness in the lateral region of the abdomen of adult males, but he did not refer to such cells in his later work on the two species of Pediculus. Graber (1872:152) also described, in Phthirius, cells with a greenish, transparent, viscous content and usually with two distinct nuclei. In *Linognathus vituli (Haematopinus tenuirostris)* Ströbelt (1882, English trans. 1883:90) found that "a fine and delicate membrane envelops the yellowish green, finely granular contents, which readily allow two nuclei to be recognized," while in the abdomen he saw small, globular cells with darker-colored contents. Nuttall (1918:378) has also mentioned these green cells as appearing in Phthirius when the insect attains sexual maturity. He criticizes the statement of Oppenheim (1901) that the pigment is formed by a ferment in the salivary glands and is deposited in the insect's fat-body, and states that the significance of the pigment is yet to be determined. In sections through mature lice these cells are found lying among the fat cells in the lateral regions of the abdomen. They are much smaller than the fat cells, and have, as a rule, only one nucleus with a well-defined nucleolus, although two nuclei have sometimes been seen. Their cytoplasm is filled with granules which stain a neutral tint as compared with the positive tint taken by the granules in the fat cells. The structure and position of these green cells suggest their interpretation as oenocytes, or further investigation may prove them to be discriminated nephrocytes such as Nuttall and Keilin (1921:184) have just described in Pediculus.

THE REPRODUCTIVE ORGANS

Male

Mjöberg (1910:226-229) was the first to give an account of the male reproductive organs of *Haematopinus suis* Leach. He interpreted the male copulatory apparatus and introduced the following nomenclature for the different parts: (1) the *basal plate*, lying within the body, articulating distally with more or less free structures, the ejaculatory duct always passing dorsal to it; (2) the *parameres* (a term used first by Verhoeff in relation to Coleoptera, and quoted by Mjöberg), strongly chitinized parts articulating on the distal part of the basal plate; (3) the *preputial sac*, surrounding the penis and the distal part of the ejaculatory duct and appearing to be attached to the distal part of the basal plate between it and the parameres. Mjöberg suggested that the sac, like the penis, may have originated from an invagination of the ninth and tenth intersegmental cuticula. He mentioned the mesodermal organs very briefly, giving most of his description to the ectodermal parts, which he figured with the penis both at rest and ejected.

With the exception of Strobelt, the earlier workers dealt exclusively with the lice infesting man. Swammerdam did not describe the male reproductive organs; the forty specimens he studied were females. Leeuwenhoek (1695:387, and 1697 187 [English trans. 1807:163]) first discovered the male, but regarded the penis as a sting. Gaulke (1863) thought the penis was an ovipositor for inserting the eggs under the skin. Landois (1864 17–21 and 1865a 52–54) described and figured the male reproductive organs of *Phthirius inguinalis* and *Pediculus vestimenti*. Graber (1872 158–159) referred to the work of Landois, and dealt briefly with the structure of the seminal vesicles and the copulatory apparatus, suggesting that the latter was a much more complicated organ than Landois had thought. Strobelt (1882, English trans. 1883:99) described the male generative organs of *Linognathus vituli* (*Haematopinus tenuirostris*) very briefly and incompletely.

More recent work on the genitalia of the lice affecting man has been done by Pawlowsky (1908), Patton and Cragg (1913), Müller (1915), and Nuttall (1917 a). The work of the last-named is the most complete account yet published of the copulatory apparatus of the Pediculidae. It does not include the internal reproductive organs. According to

Nuttall (page 304 of reference cited), " the essential parts of the apparatus are: (1) the basal plate, (2) the dilator (parameres), (3) the vesica penis [preputial sac], including its rib or strut, statumen penis, embedded in its wall, (4) the penis, and (5) the ductus ejaculatorius." In the preceding year Cummings (1916:257) had given the following explanation of the terminology used in describing the male copulatory apparatus of Siphunculata (Anoplura) and Mallophaga:

> In almost all Anoplura and Mallophaga, it is easy to recognise at once the basal plate and the parameres. The basal plate — probably double in origin as two longitudinal apodemes — is a chitinous lamina usually, if not always, longer than broad, to the posterior lateral angles of which are articulated the two chitinous appendages known as parameres. Between the parameres is the mesosome, the parts of which are not so readily made out unless a specimen be carefully dissected. Fundamentally, the mesosome is a sac — the enlarged and extrusible end continuous with the ductus ejaculatorius. This sac — called by Mjoberg " the preputial sac " — presents two regions of chitinisation — a distal and a proximal. At the distal end is the rod of the penis or virga, with frequently a splint on each side called the telomere, and one below — the hypomere.* At the proximal end are the endomeres, usually strongly chitinised bands or rods, one on each side, supporting the membrane of the sac, of which they are only local thickenings. The whole of the genitalia exhibit enormous variety in form, and the mesosomatic parts in particular are occasionally so much modified that it becomes difficult to recognise their conformation to the general plan just sketched out above. For example, in many Philopterids, such as Docophorus, no sacular portion of the apparatus is recognisable, and the distal chitinisations lie well back within the proximal, the whole forming a solid and compact mesosome. The above terms are, therefore, adopted solely for convenience of description.

* For these terms first applied to specialised Philopterid forms, see Waterston, Annals of the S. Afr. Mus., vol. x, pt. 9, 1914, p. 279.

In the hog louse the mesodermal reproductive organs of the male (Plate LXIV, 1) consist of two pairs of testes, slender vasa deferentia, seminal vesicles, and a long ejaculatory duct, and the ectodermal organs (Plate LXIV, 1 and 2) of a penis, a vesica penis, a basal plate, and parameres.

The testes are oblong-ovate with somewhat bluntly rounded ends, and the individuals of each pair touch at one end, where each opens into its vas deferens, which almost immediately unite to form a single canal. The testes lie on the dorsal wall of the mid-intestine between the metathorax and the posterior border of the fifth abdominal segment. Their free ends point respectively cephalad and caudad, and the left pair frequently lie a little anterior of the right. The vasa deferentia are long, very slender tubes lying coiled upon themselves and then passing backward to the region of the eighth abdominal segment, where they pass into the seminal vesicles just below the rectum. The latter are closely apposed to the wall of the mid-intestine and pass directly cephalad to

the anterior border of the fourth segment, where they turn ventrad and slightly caudad, appearing as a blunt angle on the ventral wall; again passing laterad and caudad, they turn cephalad at the posterior border of the seventh abdominal segment and cross the ventral wall parallel to the posterior arm of the above-mentioned angle, turning caudad about the anterior border of the third segment. In the region of the fourth segment they unite to form the single ejaculatory duct, which crosses the mid-intestine parallel to the last loop of the vesicles and is easily recognized by its marked musculature. Near the anterior end of the basal plate the duct loses its thick muscular wall and becomes a thin-walled muscular tube which is twice folded upon itself and then passes along the median line dorsad of the basal plate through the wall of the vesica penis into the chitinous penis.

A study of the copulatory apparatus of Haematopinus reveals a general resemblance to that of Pediculus and a much more detailed resemblance to that of the more closely related *Linognathus limnotragi* Cummings. The basal plate (Plate LVIII, 9, and Plate LXIV, 1, 2, and 3) lies within the ventral body wall and is much longer than broad, extending cephalad to the anterior border of the sixth abdominal segment. Its proximal end is rounded; it appears to consist of two halves joined along a median suture, which indicates its probable double origin, according to Cummings, as two long apodemes. Its anterior edge is weakly chitinized. Then follows a region of strong chitinization for muscle attachment, where there are two small apodemes along the median line, one dorsal and one ventral. The median chitinization soon disappears, but the lateral continues as stout borders ending in knoblike enlargements with which the parameres articulate. In cross section the plate is seen to consist of two lamellae, a dorsal and a ventral, and anteriorly these are fused along their lateral borders. In the region just anterior to the articulation of the parameres the lamellae become slightly broader and the two surfaces separate from one another. The inner, or dorsal, lamella grows up and closely surrounds the dorsal wall of the vesica penis, and on its lateral regions the parameres develop as chitinous thickenings. The outer, or ventral, lamella grows up surrounding the whole copulatory apparatus, and at its dorsal lateral borders forms a deep fold on each side for muscle insertion (Plate LXIV, 1 and 5). Such an outgrowth of the basal plate was not seen by Mjöberg,

and according to Nuttall is not present in Pediculus. Cummings (1916, 260) has described a somewhat similar condition in *Linognathus limnotragi* Cummings in which the parameres

> are of a remarkable type. Proximally they are broad blade-like pieces which meet each other (but do not fuse) beneath the mesosome in a fairly long median groove, then dorsally wrap themselves around the mesosome lying between them, forming a kind of sheath, from the end of which the penis projects, and, like the somewhat narrower distal ends of the parameres, curls up dorsalwards.

The parameres are two strongly chitinized regions on the lateral walls of the dorsal lamella of the basal plate, and articulate anteriorly with its lateral processes in the region of the seventh abdominal segment (Plate LXIV, 1, 2, 3, and 5). They are boat-shaped structures, with the keel external and lateral, and can be seen through both dorsal and ventral aspects. Distally they almost meet on the median line and proximally they diverge. The distal points appear to be less strongly chitinized than the remainder of the structure. In feeding experiments males approaching females were frequently seen to protrude and withdraw the parameres.

The vesica penis (preputial sac of Mjoberg, mesosome of Cummings), when lying within the body, rests within the upper lamella of the basal plate, its walls are thrown into folds (Plate LXIV, 1 and 3), and its anterior part is invaginated within the more posterior part. When ejected (Plate LXIV, 3 and 4) it passes backward and slightly downward for about half its length, when it bends slightly upward again. It is from one-half to three-fourths of a millimeter long and at its widest posterior part is approximately half as wide as its length. At its distal end on either side, directly on the median lateral line, are two small lobes covered with teeth, as is the whole sac with the exception of an area on the ventral surface near the proximal end. The thin, smooth wall of the sac surrounds the penis like a sheath for one-half of its length from the point of branching to the tip. It points directly dorsad. At its distal end the sac appears to be continuous with the basal plate. Above the copulatory apparatus and between it and the anal opening is the pregenital fold. No postgenital fold is present, unless the dorsal and ventral lamellae of the basal plate be considered as forming such.

The penis is a strongly chitinized tube made up of two half-tubes closely apposed to each other (Plate LXIV, 1 and 4). It lies within the vesica penis, its posterior pointed end turned toward the canal between the parameres, and its anterior part, into which the ejaculatory duct passes, in

line with their basal articulations. Here the chitinous structure is no longer a canal, but two divergent arms which may correspond to the statumen penis of Nuttall.

When killing lice with chloroform it was noticed that the males frequently ejected the copulatory apparatus in part or completely, and this characteristic has been utilized in the study of the musculature and movements of the apparatus. The protractor muscles of the basal plate have their origin in the ventral wall of the ninth abdominal segment where it turns dorsad, and their insertion in the anterior ventral surface of the basal plate. They form a thin plate of muscle fibers lying parallel to one another and identical in outline with the plate. When they contract, the basal plate is drawn caudad until the proximal edge lies just anterior to the boundary between segments 6 and 7, and the parameres are protruded from the sexual orifice for from one-third to one-half their length. Their dorsal aspect shows no collar-like membrane forming a sheath for the transit of the vesica penis as figured by Nuttall in Pediculus. Its place is taken by the already described upgrowth of the basal plate. They point dorsad and slightly cephalad, so that their ventral aspect is now caudad (Plate LXIV, 4). They are controlled by muscles which lie at rest alongside them and which, by their contraction along with or immediately following that of the muscles of the basal plate, hold them rigid during copulation. There are ten muscle strands on either side, of which the five posterior lie in a regular succession and the five anterior in a close group. They originate in the ventral body wall in the region of segments 6, 7, and 8. The posterior strands are inserted in the deep lateral fold of the upgrown ventral lamella of the basal plate (Plate LXIV, 5), and the anterior strands are inserted as a stout tendon in the anterior dorsal border of this upgrowth. Mjoberg (1910 189) has explained the purpose of the genital plate, at any rate in some cases, as the basis of attachment of these muscles, and his figure of *Haematopinus bufali* de Geer shows them inserted in the border of the genital plate. Cross sections through this region in the hog louse show these muscles originating laterad of the genital plate. The dorso-ventral lateral muscles of the abdomen next contract and drive the coelomic fluid caudad and into the vesica penis, which is thereby everted carrying the ejaculatory duct and the penis along with it. The thick muscular part of the duct has been drawn caudad until its posterior end lies at the level of the articulation of the

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When killing lice with chloroform it was noticed that the males frequently ejected the copulatory apparatus in part or completely, and this characteristic has been utilized in the study of the musculature and movements of the apparatus. The protractor muscles of the basal plate have their origin in the ventral wall of the ninth abdominal segment where it turns dorsad, and their insertion in the anterior ventral surface of the basal plate. They form a thin plate of muscle fibers lying parallel to one another and identical in outline with the plate. When they contract, the basal plate is drawn caudad until the proximal edge lies just anterior to the boundary between segments 6 and 7, and the parameres are protruded from the sexual orifice for from one-third to one-half their length. Their dorsal aspect shows no collar-like membrane forming a sheath for the transit of the vesica penis as figured by Nuttall in Pediculus. Its place is taken by the already described upgrowth of the basal plate. They point dorsad and slightly cephalad, so that their ventral aspect is now caudad (Plate LXIV, 4). They are controlled by muscles which lie at rest alongside them and which, by their contraction along with or immediately following that of the muscles of the basal plate, hold them rigid during copulation. There are ten muscle strands on either side, of which the five posterior lie in a regular succession and the five anterior in a close group. They originate in the ventral body wall in the region of segments 6, 7, and 8. The posterior strands are inserted in the deep lateral fold of the upgrown ventral lamella of the basal plate (Plate LXIV, 5), and the anterior strands are inserted as a stout tendon in the anterior dorsal border of this upgrowth. Mjoberg (1910, 189) has explained the purpose of the genital plate, at any rate in some cases, as the basis of attachment of these muscles, and his figure of *Haematopinus bufali* de Geer shows them inserted in the border of the genital plate. Cross sections through this region in the hog louse show these muscles originating laterad of the genital plate. The dorso-ventral lateral muscles of the abdomen next contract and drive the coelomic fluid caudad and into the vesica penis, which is thereby everted carrying the ejaculatory duct and the penis along with it. The thick muscular part of the duct has been drawn caudad until its posterior end lies at the level of the articulation of the

basal plate and parameres, and the slender part has passed along the center of the vesica, where it is surrounded by a sheath composed of slender muscle fibers. This sheath originates as two lateral bundles on the proximal border of the basal plate and is inserted as fine strands on the wall of the vesica at its junction with the penis.

At the close of copulation the protractor muscles and the body muscles relax, and the coelomic fluid passes back into the body. The vesica penis is drawn to its resting position by the contraction of the muscle sheath of the slender part of the ejaculatory duct, as well as by the contraction of many fine muscle fibers which are inserted on the surface of its anterior half and have their origin in the dorsal anterior border of the basal plate. When at rest these muscle fibers form a thick layer on the anterior region of the basal plate and a thin layer between the vesica penis and the basal plate. Some muscle fibers originate in the ventral body wall between segments 6 and 7 and are inserted in the anterior border of the basal plate, and these by their contraction bring the framework of the apparatus to its resting position.

The histological structure of the mesodermal organs shows some interesting features. The testes are surrounded by a three-layered wall — an inner slender epithelium, a very fine basement membrane, and a peritoneal wall in which there is no pigment. Fat bodies are closely apposed to the dorsal surface of the testes, and among them, as also in the peritoneal wall, tracheoles are very numerous. The contents of the testes consist of cells and developed spermatozoa, which for the most part lie in clusters of from six to twelve individuals. This is similar to the finding of Landois (1865 a:53) in Pediculus, and is common in insects. Each spermatozoon has a rod-shaped nucleus in the head, which takes the hematoxylin stain so intensely as to appear black. Anterior to the nucleus can be distinguished a small area of cytoplasm staining a bright pink with eosin just as the tail stains. No middle piece can be distinguished. These clusters of spermatozoa are in that half of each testis which lies next to the vas deferens, and appear to rest in a matrix of nutritive cells with very [illegible] staining nuclei. The remainder of each testis is filled with cells [illegible] of the different zones of development. At the base there is a very small cluster of spermatogonia, followed by spermatocytes of both orders in process of division and reduction, and then a small section of sperm[illegible]ds.

The remaining mesodermal structures are slender tubes varying in diameter. Seen in cross section (Plate LXIII, 3) the inner layer of their wall is composed of epithelial cells resting on an exceedingly fine basement membrane. Outside this is a thin, structureless layer, the true nature of which has not been determined. The anterior half of the ejaculatory duct is surrounded by a strong wall of circular muscle fibers, among which are also, toward the posterior end, strands arising at right angles to the duct wall and passing to the outer edge of the circular fibers. Nuttall (1917 a 307) attributes this strong development of muscle to the force necessary to drive the spermatic fluid down the long, slender part of the duct.

The epithelial cells lining the vasa deferentia are small and somewhat flattened, and have a straight surface in the lumen. The anterior sections of the seminal vesicles act as a reservoir for the developed spermatozoa, and there, as in the sections of the vasa deferentia, they can be seen. The epithelium of the region is regular and columnar, and the nuclei, which are circular and have a well-defined nucleolus, lie near the base of the cells, of which the cytoplasm contains many dark-staining granules. Lower in the tubes the cells lose their clearly defined inner borders and appear finely granular, while a secretion which stains a deep pink with eosin surrounds the spermatozoa. This secretion soon takes a definite form and is oval in outline, and, in appearance, not unlike a cross section of an orange or the illustration of the "Magenscheibe" given by Landois (1865a Pl. IV, fig. 8), and it contains minute vacuoles (Plate LXIV, 6). These suggest spermatophores, but in section no spermatozoa could be seen within them. Still farther along in the vesicles the inner borders of the cells project into the lumina as blunt, thumblike processes, which are slightly pink in sections stained with hematoxylin and eosin, while the remainder of the cell is dark blue. No cell walls are seen and the cells are evidently in active secretion. The clearly defined "spermatophores" now become markedly vacuolated and gradually lose all semblance of a definite form. Probably this secretion acts as a solvent. In the anterior part of the muscular section of the ejaculatory duct the cells are small, but in the posterior part the epithelium is much thickened and has a markedly glandular appearance. From many of the cells of the vesicles and the ejaculatory duct, slender processes project into the canals and even directly into the central mass of secretion, while in some parts of

the duct they interlace, giving the appearance of a network near the epithelium. The slender part of the ejaculatory duct has a small, round-celled epithelium, but in one quarter of the wall it is thickened and projects into the lumen as a more or less blunt cone, which, in the passing of the duct to the penis, forms its dorsal wall.

In gross dissection of the parts no accessory glands have been found. Patton and Cragg (1913:559) describe and figure small glands in *Pediculus vestimenti* at the junction of the vasa deferentia with the seminal vesicles, but such are not present in Haematopinus. Nuttall (1917 a:308) mentions the accessory glands of Pediculus as lying on the muscle of the dorsal surface of the basal plate and undergoing passive movement along with the ejaculatory duct and the penis at the extrusion of the copulatory apparatus, but no such glands have been found in Haematopinus. It may be that the place of accessory glands has been taken by the enlarged glandular epithelium of the different parts of the ejaculatory duct.

Female

From the work of Landois (1864:14 and 1865 a:48) it has long been known that the Pediculidae possess polytrophic egg tubes. Graber (1872:159) differed from Landois in his conception of the egg tubes, and described them as telotrophic like those of the Hemiptera but gave no figures, and subsequent work has shown him to be wrong. Strobelt (1882, English trans. 1883:94) made the earliest reference to the ovaries of *Haematopinus suis*, and he described them as bilocular. His findings in regard to the structure of the tubes and the development of the eggs confirmed the work of Landois. The classic work on the ovaries of Siphunculata (Anoplura) and Mallophaga is that of Gross (1906:347) in which he showed the close resemblance between the two groups. He studied four species, of which *Haematopinus suis* was one, and described in detail the gross anatomy and histological structure of the ovaries and the development of the egg. Mjoberg (1910:253) cited the work of Gross but did not himself mention the female reproductive organs of the hog louse. The female reproductive organs of the Pediculidae affecting man have been described by Pawlowsky (1908), who illustrated his work with transverse and longitudinal sections (Pl. II and III, figs. 1–12, of reference cited) but included no drawing of the gross anatomy; by Patton and Cragg (1913:560), who figured and briefly described the

organ; by Müller (1915), who also showed a number of figures; and by Peacock (1916). Nuttall (1917 a:312) described the copulatory apparatus.

The essential reproductive organs of the female are the paired ovaries and their oviducts, with the colleterial glands. The remaining parts are the uterus and the vagina (Plate LXV, 1). In the hog louse neither spermatheca nor bursa copulatrix is present.

The ovaries are clustered, consisting of five egg tubes on each side, and this number seems to be constant in the Siphunculata according to the different workers in the group, but the number of egg chambers in each tube differs in the various species. Each egg tube consists of a terminal filament, a terminal chamber or germarium, and as a rule two egg chambers or vitellaria although three are sometimes seen. The fine terminal filaments of each ovary of a pair unite, and pass as a single filament above the mid-intestine into the fat cells and their tracheoles. Graber (1872:159) alone, among the earlier workers, thought that three terminal filaments, or vessels as they were then called, passed from each egg tube; but, as Gross (1906:350) suggests, he probably confused tracheae with terminal threads. The ovaries lie in the abdominal cavity on each side of the mid-intestine, and in the region of the sixth abdominal segment they fuse to form a short common oviduct on either side. They pass into the uterus at the anterior border of the seventh segment after receiving the colleterial glands, which are large, trilobed glands with convoluted edges. Their anterior lobes, pointing cephalad, lie along each side of the mid-intestine under the lateral borders of the ventral abdominal muscle plate, and extend to midway between the posterior and anterior borders of segment 4; the posterior lobes are shorter, and, pointing caudad, extend just within the anterior border of the eighth segment; the lateral lobes surround the oviducts and the mid-intestine near the anterior border of segment 7.

The uterus is surrounded by a stout muscular wall which, as Landois (1865 a:51) first pointed out, is made up of circular as well as longitudinal fibers. After receiving the oviducts it passes caudad through segment 7 into segment 8, then bends back along itself just into segment 7, where it again turns caudad describing a semicircle, so that the point of its passage into the short, thin-walled vagina lies on its own spiral. The meaning of its length and musculature is revealed in examining specimens having a mature egg in the uterus. It is then a long, straight, and wide tube,

whose anterior border lies approximately on the anterior border of the fourth segment.

The structure of the female copulatory apparatus is much simpler than that of the male. It is situated in the last three segments of the body, and the external indications of sex are the shape of the abdomen, two triangular chitinous plates on the dorsal surface of segment 9 (which ends in two pointed lobes), and the gonopods on the ventral surface of segment 8. The gonopods (Plate LVIII, 11) are flat processes, triangular in shape. Their median free border is somewhat strongly chitinized and is set with a row of stout hairs. Anteriorly they are joined by a fold of the integument which projects caudad in two blunt points. As has already been said, they appear to have arisen as an infolding of the integument of the segment. The sexual orifice is on segment 8 under the anterior border of the gonopods. It leads directly into the vagina, a thin-walled chitinous sac lying close to the ventral body wall and at its anterior end passing into the uterus ventrad of its semicircular coil. In Pediculus the walls of the vagina are covered with minute, outward-pointing teeth. In Haematopinus no teeth could be seen on the vaginal wall in gross preparations treated with potash and mounted in balsam.

A plate of closely set muscle fibers originates in the anterior border of segment 7 immediately posterior to the ventral abdominal muscle plate, and is inserted in the anterior border of the gonopods. The contraction of these muscles raises the gonopods and brings the sexual orifice and the vagina into position for copulation. Muscle fibers originating in the lateral wall of the vagina and in that of the uterus near its passage into the vagina, are inserted in the sternite of segment 9, and by their contraction draw the vagina and the uterus to their resting position.

The histological structure of the ovarian tubes at different stages of development has been thoroughly studied and described by Gross (1906: 352–364), and a brief résumé of his work is here inserted. There is no peritoneal wall surrounding the egg tubes, and the tunica propria (basement membrane) is unusually well developed. In the terminal threads of adult females the content consists of a homogeneous granular protoplasm which Gross regards as degenerated remains of the cells to be found in younger stages. Landois (1864: 16) had seen these cells also in the terminal chamber of Phthirius, and he considered them as specific yolk-forming elements and hence the terminal chamber of the one-egg tube

as a true yolk chamber. This chamber remains small, there is no boundary between it and the terminal thread, and its epithelium is composed of small nuclei between which cell boundaries are seldom seen. In young individuals the chamber contains only a few cells besides the epithelial nuclei (Plate LXVI, 4), while in older animals the cells are quite degenerated and are broken up into scattered fragments until finally only epithelial nuclei remain and these have migrated into the interior of the chamber (Plate LXVI, 7). In every case Gross found a zone of transversely arranged epithelial cells behind the terminal chamber. Such a zone is characteristic of telotrophic egg tubes and has not been found in any other group having polytrophic egg tubes. In Haematopinus it is very short and in some cases is represented only by a row of much degenerated epithelial nuclei, distributed in the longitudinal direction of the egg tube. In the egg chamber (Plate LXVI, 9) there is a definite number and arrangement of nutritive cells. There are five of these, and the odd one lies in the apex, with the others in two successive rows immediately behind. The nuclei of all are irregular in outline. Such an arrangement was seen by Landois (1865 a 48) in Pediculus. The two hindmost nutritive cells push into the plasma of the egg, and there is seen a layer of dark-stained, ball-like, little nuclei which are the nutritive substance introduced from the cell to the egg for the formation of the yolk. In the older individuals the follicle epithelium is clearly seen to be of two kinds. That surrounding the nutritive cells is thin and flat, having few nuclei and no distinct cell walls; while that surrounding the egg chamber is made up of deep cylindrical cells closely apposed on one another and containing cylindrical nuclei with an elongated nucleolus. The mitosis seen in the epithelium of younger stages has now given place to amitosis, and finally each cell contains two nuclei which lie behind each other in the longitudinal axis of the cell (Plate LXVI, 10). Gross has never seen cell division following the amitotic division of the nuclei, and in the light of more recent researches this nuclear division is to be regarded rather as a redistribution of nuclear material than as a true amitosis. Behind the egg cell the follicle cells are hemmed in by a collection of dark nuclei similar to those behind the nutritive cells, and cell boundaries are wanting at this point; both these facts support the view that in Haematopinus, as in so many other cases, the follicle epithelium cooperates in the formation of the yolk. The

successive egg chambers are connected by short stalks of epithelial cells, apparently a continuation of the follicular epithelium.

The egg tubes of each side pass into a short oviduct which receives the wide conduit of the colleterial gland before passing into the uterus. The wall of the oviduct is made up of a thin muscular layer, a fine basement membrane, and small epithelial cells with an inner delicate chitinous lining; that of the colleterial gland consists of a peritoneal membrane, a thin basement membrane, and large columnar epithelial cells with large nuclei (Plate LXV, 2). These large epithelial cells secrete the cement which glues the eggs to the bristles, and in sections stained with hematoxylin and eosin the secretion is seen as a pink, homogeneous, more or less vacuolated mass, while with iron hematoxylin it appears dark brown or black. The uterus receives the oviducts laterally and somewhat posterior to its apex. In this region the muscular coat is only moderately developed the epithelium and its basement membrane are clearly seen, and the chitinous lining is smooth (Plate LXV, 3). Posterior to the point of entrance of the oviducts the wall is thrown into deep folds and the muscular outer coat is very highly developed. The epithelial cells are small and no distinct cell boundaries are seen. The chitinous lining is thrown into innumerable sharp convolutions resembling moderately long, sharp teeth (Plate LXV, 4), which, posteriorly in the region of the coil, appear as blunt, rather flattened teeth (Plate LXV, 5 and 6). From sections made through a uterus containing an egg, it appears that these teethlike projections retain their form when the uterus is fully expanded.

The earliest description of the egg of the hog louse is that of Leuckart (1855:140–141). He recognized the presence of a third chorionic layer, but without sections it was impossible to get a true conception of the structure. He figured a piece of the shell, showing it to be provided with innumerable canals running perpendicular to the surface of the chorion. Strobelt (1882, English trans. 1883:96–97) described briefly the egg of *Linognathus vituli* (*Haematopinus tenuirostris*), citing Leuckart and Landois. The most complete and accurate description is that of Gross (1906:364–377), who found, in the eggs of Siphunculata (Anoplura) and Mallophaga, structures so similar as to indicate close relationship between the two groups. Mjoberg (1910:257–262) refers to the work of Gross and describes briefly the eggs of several additional species of Siphunculata (Anoplura) and Mallophaga.

The follicle epithelium of the egg chamber secretes first the vitelline membrane, which in this case is also the cell membrane of the egg, and then the chorion. According to Gross, of whose work the following is a résumé, the formation of the chorion begins at the posterior end and a thin endochorion and a thicker exochorion are formed. The former appears striated in section and may be porous. The follicle cells are somewhat convex on their inner surface and an imprint of this is left on the exochorion. Up to this time their nuclei have been lying toward their inner surface, and the formation of the epichorion (exochorion of Leuckart) begins as a constriction between the nuclei, and in the indentations so formed appear small, rather regularly rhomboid, chitinous structures. (The egg shell is not formed of true chitin, since it is soluble in potassium hydroxide.) By further constriction of the epithelial cells between the nuclei a system of hollow cavities in communication surrounds the egg, and these become almost filled by a deposition of chitin forming a distinct chitinous lamella (Plate LXVI, 21 and 22). Up to this point a nucleus has rested on each side of the constriction, but now the one between the epi- and exochorions passes through the canal leaving only a tip of protoplasm (Plate LXVI, 23 and 24). The epichorion now moves closer to the eggshell proper, and the pores assume the appearance of rather long canals (Plate LXVI, 25, a); so that looked at from the surface (Plate LXVI, 26), the epichorion appears pierced by numerous canals perpendicular to its surface (Leuckart, 1855: 140; stomata of Stevenson, 1905: 16). Between these pores is a network of three-sided cavities. During this development the staining properties of the epithelium have undergone a change: the protoplasm takes a deep stain, while the nucleoplasm has become transparent and the nucleolus no longer shows great affinity for stain.

On the operculum there is no epichorion formed and the exochorion is much thickened (Plate LXVI, 25, b). The chitin formation extends down the sides of the epithelial cells, but it is an outgrowth from the exochorion and not a separate formation. There are polygonal areas on the lid surrounded by a network whose ridges are much deeper than those on the egg, but, as there is no epichorion here, the two parts do not differ in level.

The epithelial cells now rapidly degenerate, and characteristic, very darkly stained structures, like broken circles, are seen in their protoplasm. On the operculum these are attached to the ridges and extend lengthwise

so that a fork is formed, between the prongs of which are transverse ridges (Plate LXVI, 28). These structures have no very regular character, and Gross could not determine whether they originated as separate rings or as lamellae. In the vicinity of the furrow between the egg and the operculum the appearance is distinctly modified (Plate LXVI, 27, b). Here the branches of the network are themselves forked and their prongs are extended as longitudinal rings; also, the transverse rings are more numerous and irregular. Behind the operculum there is still another structure. Over the network of the exochorion, and at first without any connection with it, is formed a characteristic trellis of longitudinal and transverse rings, having as a groundwork a narrow, undulating band whose curved edges lie always on a furrow of the epichorion. The whole is then set through with transverse parallel rings, some of which are found also between the epichorion network. Directly behind the opercular furrow the chorion extends as two specially large projections which bend forward and are forked at their outer ends (Plate XLVI, 27, a). These are two lamellae, which extend around the whole circumference of the egg, overarching the furrow and protecting it. In the fully developed egg (Plate LXVI, 29) the rings are said to be made of chitin and to have become a part of the chorion. The remainder of the epithelium is now an amorphous mass and is the so-called egg-white layer around the egg, of which Gross says (page 370 of reference cited): "Auch dieser Umstand, dass der Follikel schliesslich sich zur Eiweisshülle umbildet, ist, soviel ich weiss, ohne Analogon unter den Insecten." The epichorion is connected with the exochorion anteriorly at the opercular ridge and posteriorly at the egg stigma, a complicated structure whose significance is not clear. A diffusion of air through the pores cannot take place because of the egg white. An interchange of gas cannot take place, although the space between the exochorion and the epichorion contains a quantity of gas; rather is this chamber of gas to be regarded as a warm covering for the egg, or it may serve as a protection against injury from blows to which eggs attached to the hair of animals are exposed.

In the egg of the hog louse the micropyles are not indicated by any special formation. In sections they can be seen as simple canals, narrowing somewhat at their inner ends, in the vicinity of the operculum. Leuckart (1855, 141) did not state their number; according to Gross (1906, 371) there are at least thirty.

At the posterior pole of the egg is a very characteristic structure (Plate LXVI, 34), to which Graber (1872:165) gave the name "Eistigma." The earliest description of this structure is that of Leuckart (1855:139, 141), who observed it on the eggs of *Pediculus capitis* and *Haematopinus suis*, and it was seen also by Landois (1864:15) on the egg of Phthirius. Gross (1906:372) has given the first detailed description of it and figured its structure. The egg stigma forms a roundish swelling on the chorion and is pierced by numerous thin-walled canals, which narrow toward their inner ends and converge to one side. Gross studied its formation in detail, and in young stages found the egg follicle closed by a plug extending far into the interior of the yolk, but as growth proceeds the plug becomes leveled. The nuclei are small and the inner ends of the cells are drawn to a point. These inner ends are cut off from the cells in a characteristic manner and the nucleus is drawn to the outer wall, while between them is a zone of protoplasm in which cell boundaries can no longer be recognized. Between the detached inner pieces begins the deposition of chitinous substance, and this appears as fine striae, while at the exterior, where the deposition has become more advanced, the thin, chitinous lamellae have lost their color. There are formed in the region of the stigma the endochorion and the exochorion. The stigma is now completely developed. The point formed by the pointed ends of the cells still remains attached inside, cell walls can be recognized, and it can be seen that each cell forms a canal.

No satisfactory biological interpretation has been found for the egg stigma, a structure found in no other insect order. Earlier authors advanced three views, none of which has proved satisfactory. Leuckart (1855:139) and Melnikow (1869:154) regarded it as an attachment disk; but if this were its function, why should it be pierced by canals in most cases? Kramer (1869:462) regarded it as the true micropyle; but in some species, for example Nirmus, the canals do not pass to the inner ends of the cells. Graber (1872:163) interpreted it as a means of aeration for the eggs and so named it; but in most cases it is covered over by secretion. The closing of the pores by secretion would be essential in Pediculus, since, according to Sikora (1915:530) and Nuttall (1917d:148), the embryo escapes from the egg by pumping air through its alimentary canal in order to increase the pressure in the egg and force open the operculum.

TECHNIQUE

In the laboratory the following methods of keeping lice have been tried.

Conditions	Temperature	Opportunities of feeding in 24 hours	Length of life
On laboratory table in petri dishes	Room temperature	4	7–10 days
In incubator in open vials	36°–37° C., dry heat	4	Under 24 hours
In incubator in vials having in the bottom a layer of moist cotton batting ¼–½ inch thick	36°–37° C., moist heat	4	3 days
In a gauze bag worn on the body	35° C.±	Constant	Lice would not feed through gauze
In vials plugged with cotton and gauze and carried close to the body day and night	35° C.±	3–4	Up to 35 days
As in last experiment	35° C.±	First day, 3; second to fifteenth day, 2; sixteenth to twenty-sixth day, 1	26 days

We have found the last method the best for rearing hog lice in captivity. In the glass containers, hog bristles and teased gauze were provided as a foothold.

Chloroform has been found the most satisfactory medium for killing lice both for dissection *in toto* and for sectioning. For the former purpose the lice may be preserved indefinitely in 80- to 85-per-cent alcohol, but the following fluid has been found much more satisfactory:

Distilled water	30 parts
Alcohol, 96-per cent	15 parts
Formaldehyde	6 parts
Glacial acetic acid	4 parts

This fluid was first used by Pampel (1914:298) in his work on the female Ichneumonidae, and he found that it kept the tissue soft and elastic for dissecting purposes. After chloroforming, a small slit was cut in the side of the abdomen to allow the preserving fluid to penetrate more rapidly.

Owing to the toughness of the cuticula, dissections could not be made on slides, and so the lice were fixed to the top of a thin layer of paraffin in the bottom of a watch glass and covered with physiological salt solution. Scalpels with curved blades, microscope scissors, and fine needles were used, and all dissections were made under a Zeiss binocular. After some practice the different systems could be removed intact and placed on slides in a drop of salt solution, where the parts could be arranged in the desired way and fixed in position with Bless' fluid according to the method followed by Patton and Cragg (1913.718-720). The material could then be carried through the alcohols and stained *in toto*. The best result in such staining has been obtained with Grenacher's borax carmine, the stain being allowed to act for from twenty-four to forty-eight hours. In dissecting organs for sectioning, the physiological salt solution was replaced by the medium in which the tissue was fixed.

In the study of the epithelium of the digestive tract, the alimentary tract was dissected out and prepared for imbedding in paraffin. In order to cut more than one stomach at a time, the method learned by Minchin from fellow workers in the Zoological Station at Naples in 1891, and used by Minchin and Thomson (1915 508) for sectioning the stomachs of fleas in their study of the rat trypanosome, was tried. Their method consisted of cutting thin free-hand sections of amyloid liver, arranging three stomachs on it with the anterior borders level, and fixing them in position with a drop of albumen fixative. This block could be oriented easily, but it was found more satisfactory to simply imbed single alimentary tracts.

In sectioning whole lice it was necessary to double-imbed in celloidin and paraffin, and three methods were followed, all of which gave equally good results. The slow method of celloidin imbedding, beginning with a thin solution and gradually increasing the thickness until the object was sufficiently permeated with celloidin to be hardened in chloroform and carried on to paraffin in the usual way, was first tried. Then, in order to shorten the period of infiltration, a modification of Gilson's rapid method (Lee, 1905:131) was substituted. At the same time the oil-

mixture method introduced by Apáthy (1912:464, 468; also Kornhauser, 1916) was used, but it gave no better results than Gilson's rapid method and involved many more steps. After double-imbedding it was found possible to make good series of longitudinal and transverse sections of 5 microns, 7½ microns, and 10 microns, in thickness.

The reagents used for fixing were Zenker's fluid, Bouin's fluid, and Flemming's weak solution. In every case the insect was chloroformed and its legs were cut off close to the thorax before it was placed in the reagent. Both the Zenker-fixed and the Bouin-fixed material were stained with hematoxylin and eosin, hematoxylin and orange G, and methylene blue and eosin. In addition the Bouin-fixed material was stained with Mallory's anilin-blue connective-tissue stain, a combination used by Kingery (1916: 292) in studying the intestine of the grasshopper. This stain differentiates the chitinized from the non-chitinized cuticula, the former staining red and the latter a clear blue, and also brings out strikingly the striations of the muscle fibers. The Flemming-fixed material was stained with iron hematoxylin according to the method of Heidenhain, and with safranin, a solution made of equal volumes of a water-soluble and an alcohol-soluble stain being used.

All measurements given in the text were made with an ocular micrometer valued in terms of a stage micrometer used in a Zeiss microscope fitted with an objective A, 15 millimeters, and an ocular No. 2, and having a tube length of 160 millimeters.

SUMMARY

At the close of his paper on the mouth parts of the body louse, Harrison (1916b:218) has pointed out the many resemblances found by himself and other workers between the Siphunculata (Anoplura) and the Mallophaga, particularly those of the suborder Ischnocera. The present study has served to again emphasize the general similarity in structure of the two groups, and has brought to light some structures which have not yet been described in this order.

No mention of the apodemes extending from the dorsal to the ventral surface of the thorax has been found in the literature. While the name suggested for them — the apodemes of the prothorax and the prosternum — is intended to call attention to their position in the anterior part of the thorax, it must not be forgotten that they probably originated as ventral-

nations respectively of the transverse conjunctivae between the pro- and the mesothorax and between the pro- and the mesosternum.

A second structure hitherto undescribed in the Siphunculata is found in the head, under the posterior lobes of the brain. The position and structure of this pair of bilaterally symmetrical circular bodies suggests their interpretation as the "corpora allata" of Heymons and other investigators (cited by Berlese, 1909.588, and by Schroder, 1912–13:86).

In the study of the stomodaeum and the mouth parts, the aim has been to present as accurate a picture as possible of their anatomical structure, musculature, and working. Their homology is not touched upon, because in the case of structures so far modified from the generalized type, interpretation should rest upon an investigation begun with the earliest appearance of segmentation in the embryo and continued to maturity. Cholodkovsky (1903:120) alone has touched upon this aspect, in his work on the man-infesting pediculi, whose pharynx and mouth parts are similar in plan to those of the hog louse. In none of the sections of the alimentary canal have protozoan parasites been found, and the physiology of digestion has been touched upon but briefly.

The reproductive systems and the secondary sexual characters resemble those of other members of the order, but in the female no receptaculum entering the uterus has been found. According to Harrison (1916 b:221), "in the Ischnocera, and in all Anoplura save Pediculus, a receptaculum of remarkable structure opens into this uterus by a long narrow duct, the entry of the duct into the receptaculum being marked by a conspicuous chitinous ring."

The experimental work on the biology of the species has been carried out with much care. In the acceptance of the resulting figures indicating periods in the life history, however, it must be borne in mind that in the natural habitat, with continual opportunity of feeding, these periods may be somewhat shorter.

ACKNOWLEDGMENTS

Thanks are due to Dr. V. A. Moore, of the New York State Veterinary College at Cornell University, for facilities for keeping a hog for experimental work; to the Department of Entomology of the New York State College of Agriculture at Cornell University, for the payment of the expenses connected with keeping the hog; to the Department of Animal

Husbandry of the same College for the loan of the hog; to Professor E. S. Savage, of the Department of Animal Husbandry at Cornell University, and to Drs. Carl Ten Broeck and R. B. Little, both of the Department of Animal Pathology at the Rockefeller Institute for Medical Research, for assistance in obtaining lice; to Dr. W. A. Riley, of the University of Minnesota, for a supply of man-infesting lice for comparative purposes; to Dr. S. A. Goldberg, of the New York State Veterinary College, for assistance in taking photographs; and to Professor Ulric Dahlgren, of Princeton University, for access to the library of the Department of Biology at that institution and to the piggeries of the university farms.

The illustrations were drawn by Miss Ellen Edmonson, to whom we are deeply indebted for the great care with which she has done the work.

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Memoir 11, *Lysimeter Experiments — II*, the tenth preceding number in this series of publications, was mailed on November 16, 1921

Plate LVIII

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Claws of adult (a, protrusible pad, b, joint between tibia and tarsus), 2, eggs attached to hog bristle (a, cap, or operculum, b, vitelline membrane, c, cement), 3, first instar, 4, second instar, 5, third instar, 6, sternal plate, 7, exuvia attached to bristle, 8, adult male, 9, ventral aspect of posterior segments of abdomen of male, 10, adult female, 11, ventral aspect of posterior segments of abdomen of female (a, gonopods); 12, apodeme of prosternum and prothorax attached to sternal plate

(3, 4, and 5 drawn from exuviae, to same scale as 8 and 10)

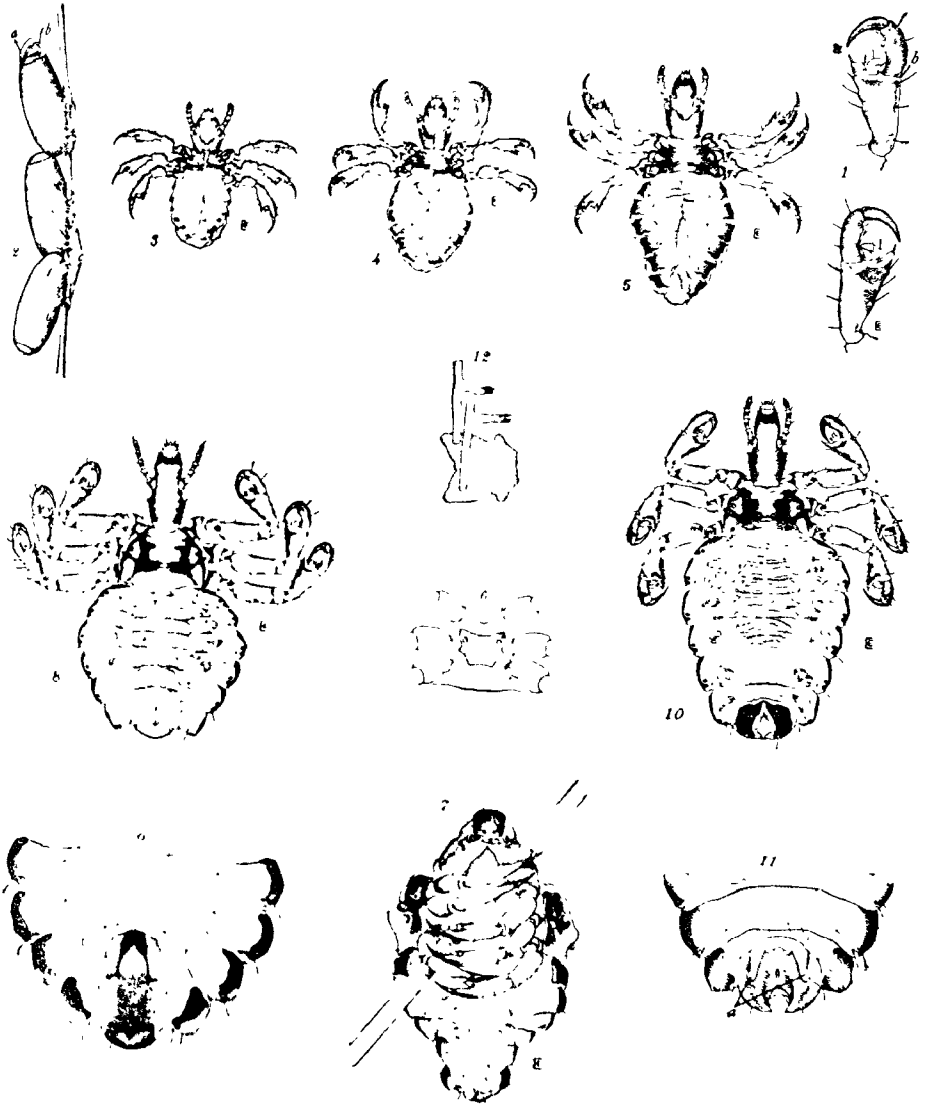

Plate LIX

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Diagrammatic representation of primary and secondary tracheae. 2, stigma, vestibule, bulla, and trachea, drawn from cleared specimen. 3, section through abdominal stigma: a, vestibule; b, lever; c, bulla; d, intrinsic muscle; e, extrinsic muscle. 4, ventral abdominal muscle plate of female, ventral aspect. 5, right lateral abdominal muscles of segment 4 of male drawn from gross dissection. 6, heart and one-half of length of aorta. a, pericardial cells. 7, transverse section through heart in region of ostium. 8, central nervous system and anterior part of sympathetic system. a, frontal ganglion; b, recurrent nerve; c, brain; d, subœsophageal ganglion; e, connectives; f, protothoracic ganglion; g, mesothoracic ganglion; h, metathoracic ganglion and abdominal ganglion; i, ventral nerves. 9, sections through tip of antenna showing multinuclear sensory cells (drawn with oil immersion).

Plate LX

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through anterior region of head just posterior to section shown in Plate LXI, 1 (a, buccal plate; b, dorsal element of piercers; c, anterior ends of pumping pharyngeal tube; l, structures corresponding to "mandibles" of Siphona; mm, muscles of these; nn, dorsal protractors of buccal plate; o, prefrontal ganglion). 2, dorsal aspect of anterior part of stomodaeum (a, buccal plate; c, pumping pharyngeal tube; g, pumping pharynx; k, pharynx; nn, dorsal protractor muscles; pp, ventral protractor muscles; qq, anterior dorsal retractor muscles; rr, posterior dorsal retractor muscles; ss, dorsal muscles of pharynx; t, oesophagus; u.u, "mandibles" of Lipoptena; vv, lateral tendon muscles; w, haustellum with buccal teeth; dilator muscles of pumping pharynx not shown). 3, ventral aspect of anterior part of stomodaeum (xx, ventral retractor muscles; other lettering as in 2). 4, ventral aspect of haustellum protruded and showing buccal teeth. 5, transverse section through anterior region of thorax, showing posterior ends of rami of piercers with their muscle attachments (a, cuticula enclosing piercers and oesophagus; b, dorsal element of piercers; d, ventral element of piercers; ee, buccal apodeme; f, aorta; k, recurrent nerve; ll, tracheae; nn, connectives; nn, posterior arms of apodeme of prothorax and prosternum; o, salivary gland between rami of piercers; t, oesophagus; v, mouth parts; b, dorsal element of piercers; c, salivary duct; dd, rami of ventral element of piercers; o, salivary gland between rami of piercers; p, anterior end of chitinous plate imbedded in floor of sheath; qq, protractor muscles of sheath and piercers; ll, ventral lateral retractors of sheath and piercers; rrr, dorsal lateral retractors of sheath and piercers; nn, posterior retractors of sheath and piercers; posterior retractors inserted in end of each ramus, not shown; sheath torn away, leaving only ventral plate and piercers, so that lateral retractor muscles appear in approximate position). 7, dorsal element of piercers (a, bulb at end of salivary duct; salivary duct and flowing piercer shown as a dotted line in proximal part only; b, ventral element of piercers (p, chitinous plate imbedded in floor of sheath). 9, anterior ends of ventral elements of piercers

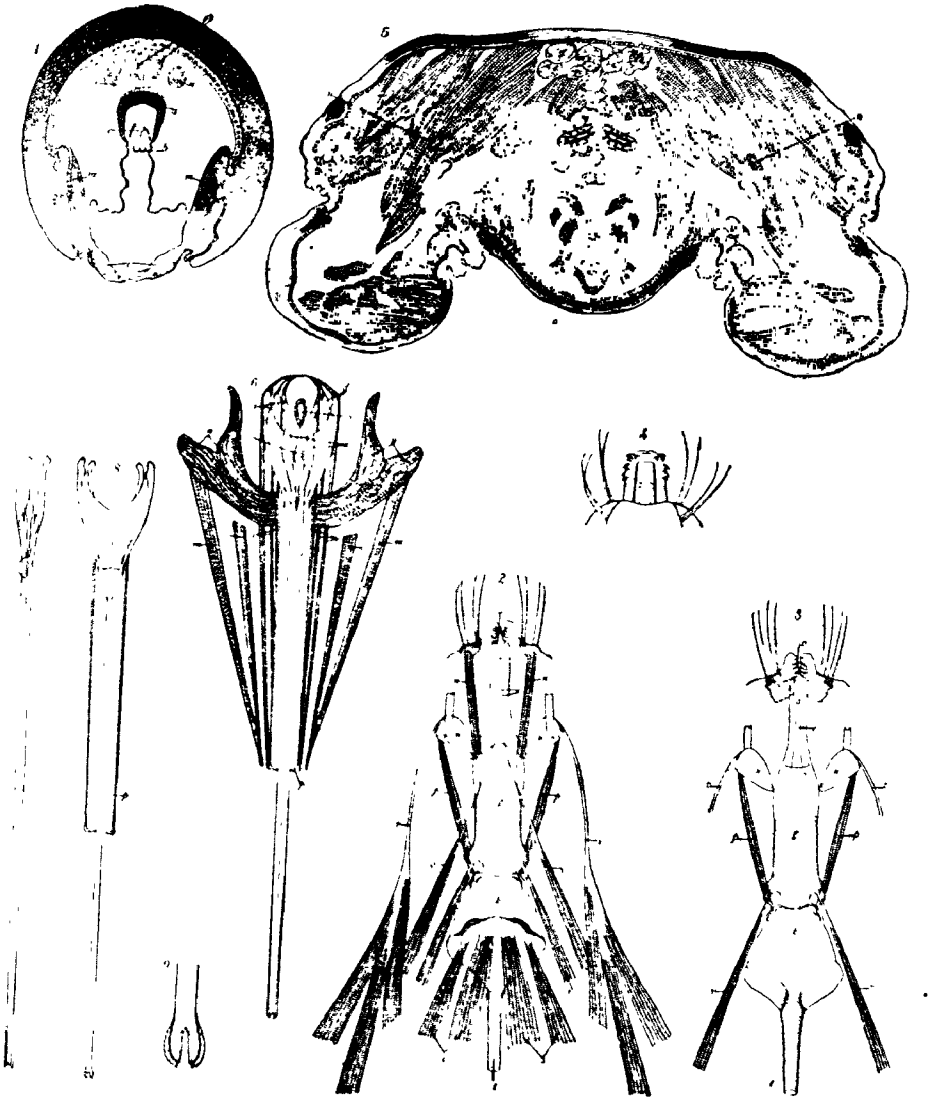

Plate LXI

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through stomodæum at anterior level of attachment of basal part of "mandibles" of Enderlein to lateral wall of head; *ba*, buccal plate; *c*, dorsal element of pterostyle; *d*, salivary duct; *e*, ventral element of pterostyle. **2,** transverse section through stomodæum at anterior level of "mandibles"; *p*, pumping pharyngeal tube; other lettering as in 1. **3,** transverse section through stomodæum at posterior level of "mandibles"; lettering as in 1 and 2. **4,** transverse section through stomodæum in posterior region of buccal plate; *aa*, posterior arms of buccal plate; *f*, ridge on dorsal wall of pumping pharynx; other lettering as in 1 and 2. **5,** transverse section through stomodæum in region of anterior dorsal chitinous plate; *g*, pumping pharynx; *h*, pterostyle sheath; other lettering as in 1. **6,** transverse section through stomodæum immediately behind anterior chitinous plate; *m*, tendons of dorsal retractors of buccal plate; other lettering as in 5. **7,** transverse section through stomodæum just after its separation from pterostyle sheath; lettering as in 6. **8,** transverse section through anterior region of pharynx; *n*, pharynx. **9,** transverse section through posterior region of pharynx behind first dorsal chitinous plate; *ll*, hollow tendons of central elevator muscles; *k*, pharynx.

(All drawings on this plate made with oil immersion and drawn to scale)

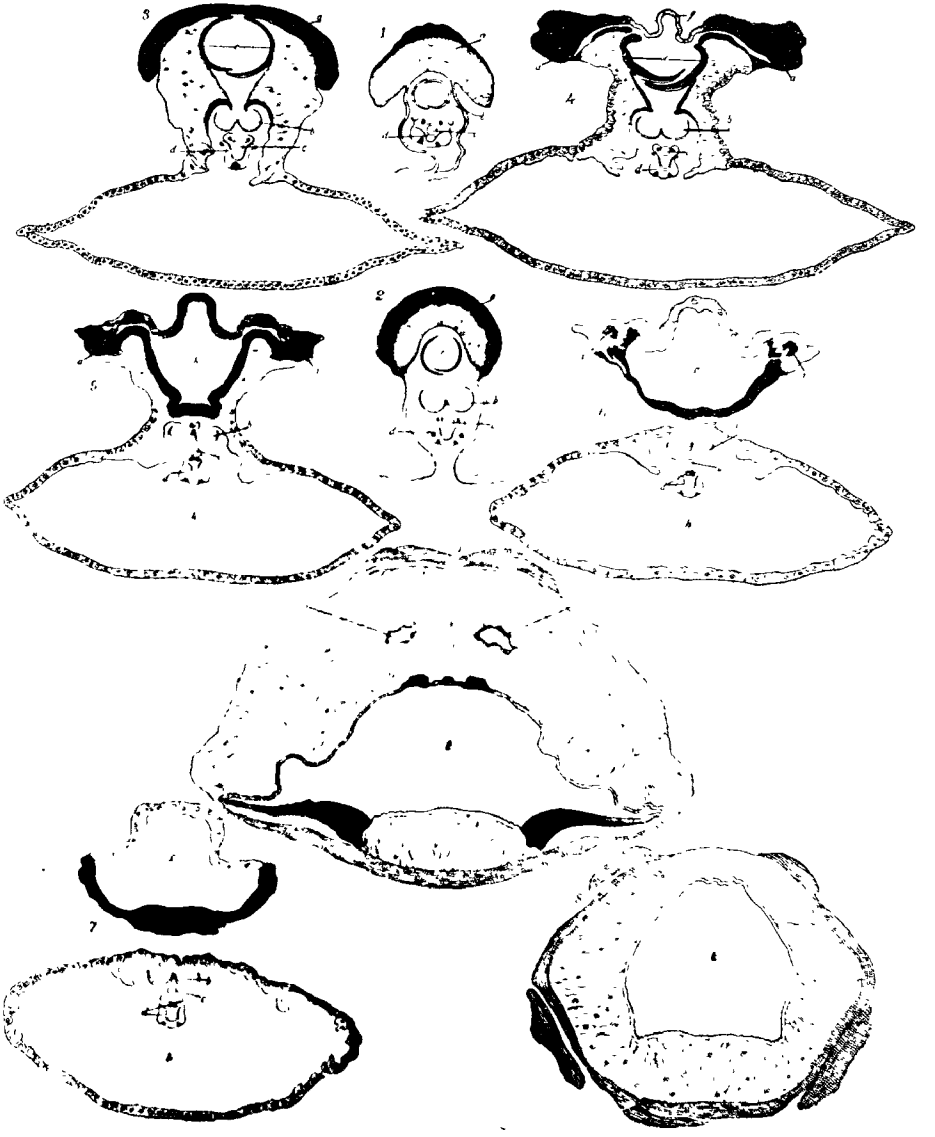

Plate LXII

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through head showing Pawlowsky's glands opening into piercer sheath (a, glands b, piercer sheath). 2, longitudinal section through Pawlowsky's gland (drawn with oil immersion). 3, salivary glands in natural position (a, ventral aspect; b, lateral aspect). 4, horseshoe-shaped gland. 5, oblong-ovate gland. 6, anterior region of horseshoe-shaped gland and duct (drawn from gross specimen with oil immersion). 7, stomach (a, oesophagus; b, mid intestine; c, small intestine; d, region of plates; e, rectum; f, malpighian tubes). 8, transverse section through region of plates. 9, transverse section through rectum. 10, longitudinal section through abdominal segment (a, fat cells, b, oenocytes).

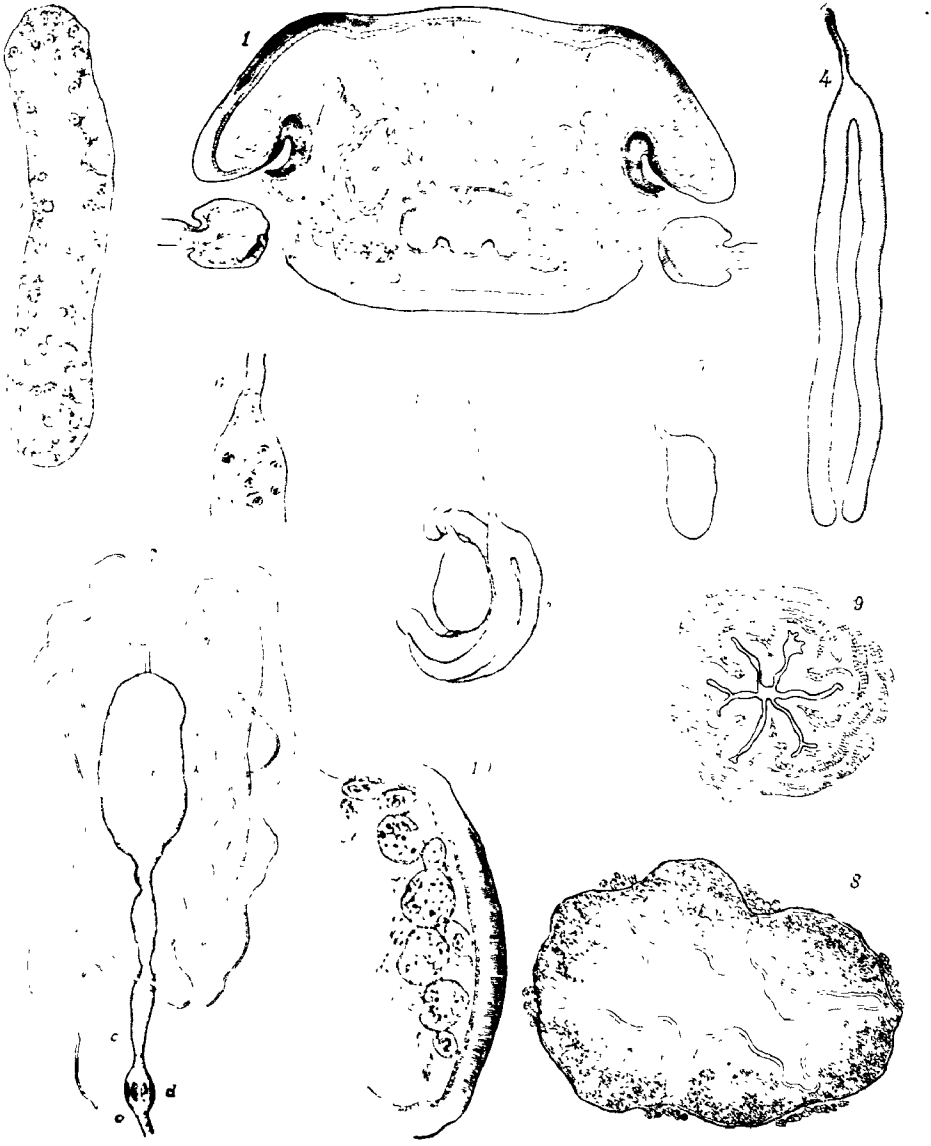
1
4
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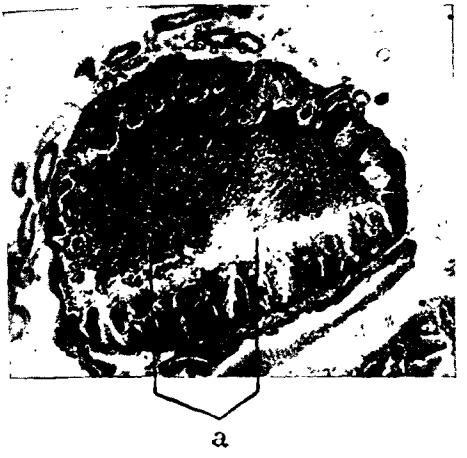
Plate LXIII

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Transverse section through stomach nine hours after feeding, x 192½ (a, region of section enlarged in 2). 2, region a of 1, x 600. 3, transverse section through intestine and reproductive organs of male, x 280. a, intestine. b, seminal vesicles containing spermatophore. c, muscular part of ejaculatory duct. d, slender part of ejaculatory duct. e, vasa deferens. f, upper region of seminal vesicles which acts as reservoir for spermatozoa. g, malpighian tubes. h, trachea.

1



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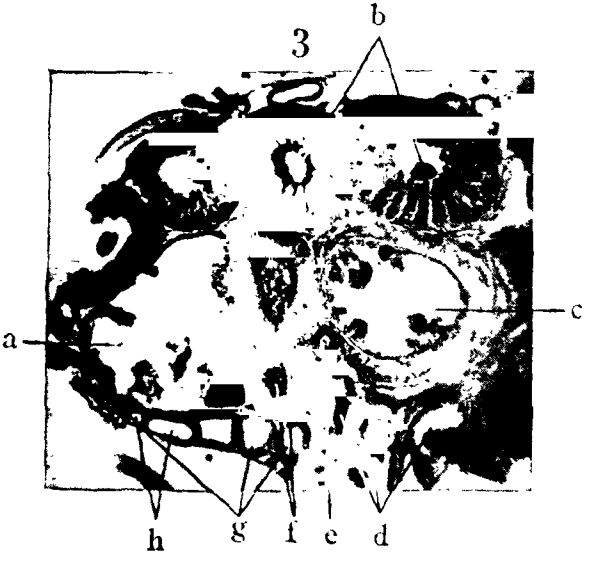

Plate LXIV

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Reproductive organs of male (a, testes, b, vasa deferentia, c, seminal vesicles, d, ejaculatory duct, e, penis, f, vesica penis, g, basal plate, h, parameres). 2, ectodermal reproductive organs of male in resting position, dorsal aspect (lettering as in 1). 3, ectodermal reproductive organs of male, vesica exserted, ventral aspect (lettering as in 1). 4, posterior region of abdomen with vesica and penis ejected, lateral aspect (B, caudal aspect; L upgrowth of ventral lamella of basal plate, corresponding to collar described by Nuttall in Pediculus, lettering otherwise as in 1). 5, transverse section through posterior end of abdomen of male (e, penis, f, vesica penis, ga, dorsal lamella of basal plate showing thickening of parameres, gb, ventral lamella of basal plate, i, muscles of parameres, j, retractor muscles of vesica, k, protractor muscles of basal plate), 6, transverse section of "spermatophore" (drawn with oil immersion)

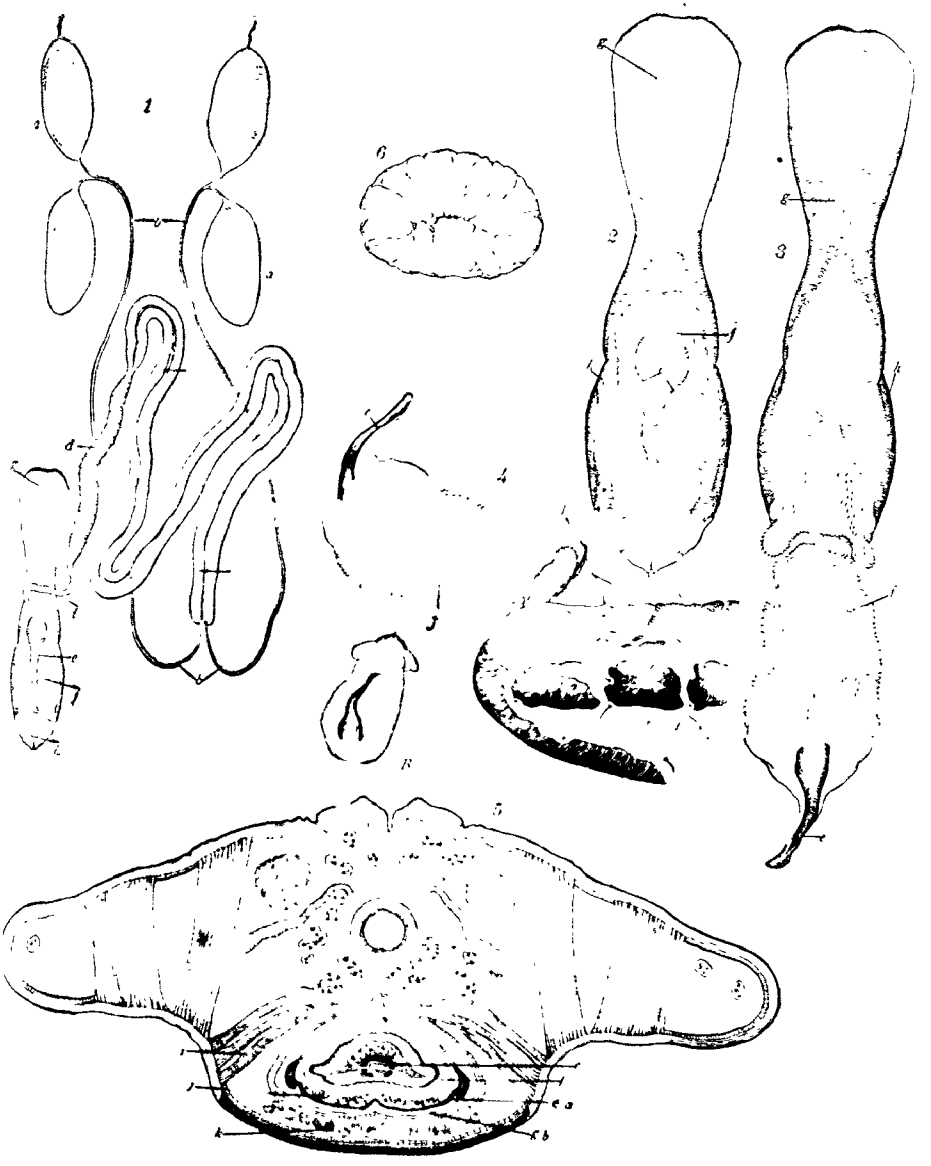

Plate LXV

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1. Reproductive organs of female (a, ovaries, b, oviducts, c, colleterial glands, d, uterus), 2, transverse section of part of wall of colleterial gland (drawn with oil immersion, a, trachea), 3, transverse section through anterior end of uterus, 4, transverse section through uterus posterior to the entrance of oviducts (a, secretion from colleterial glands), 5, transverse section through uterus in region of coil, b, teeth of intima in 5 (drawn with oil immersion)

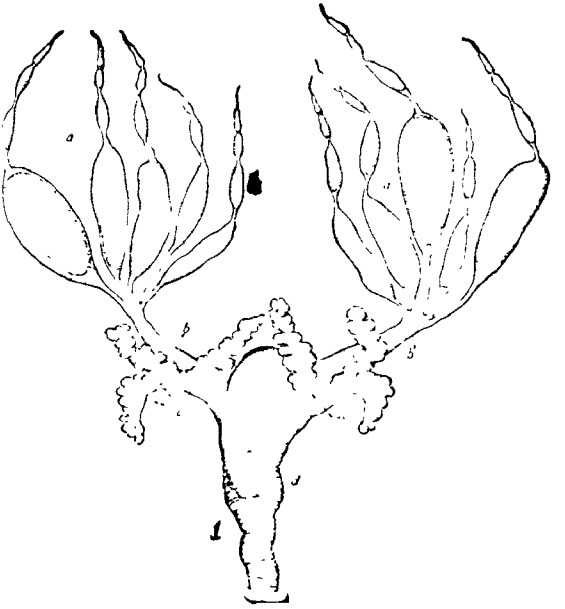
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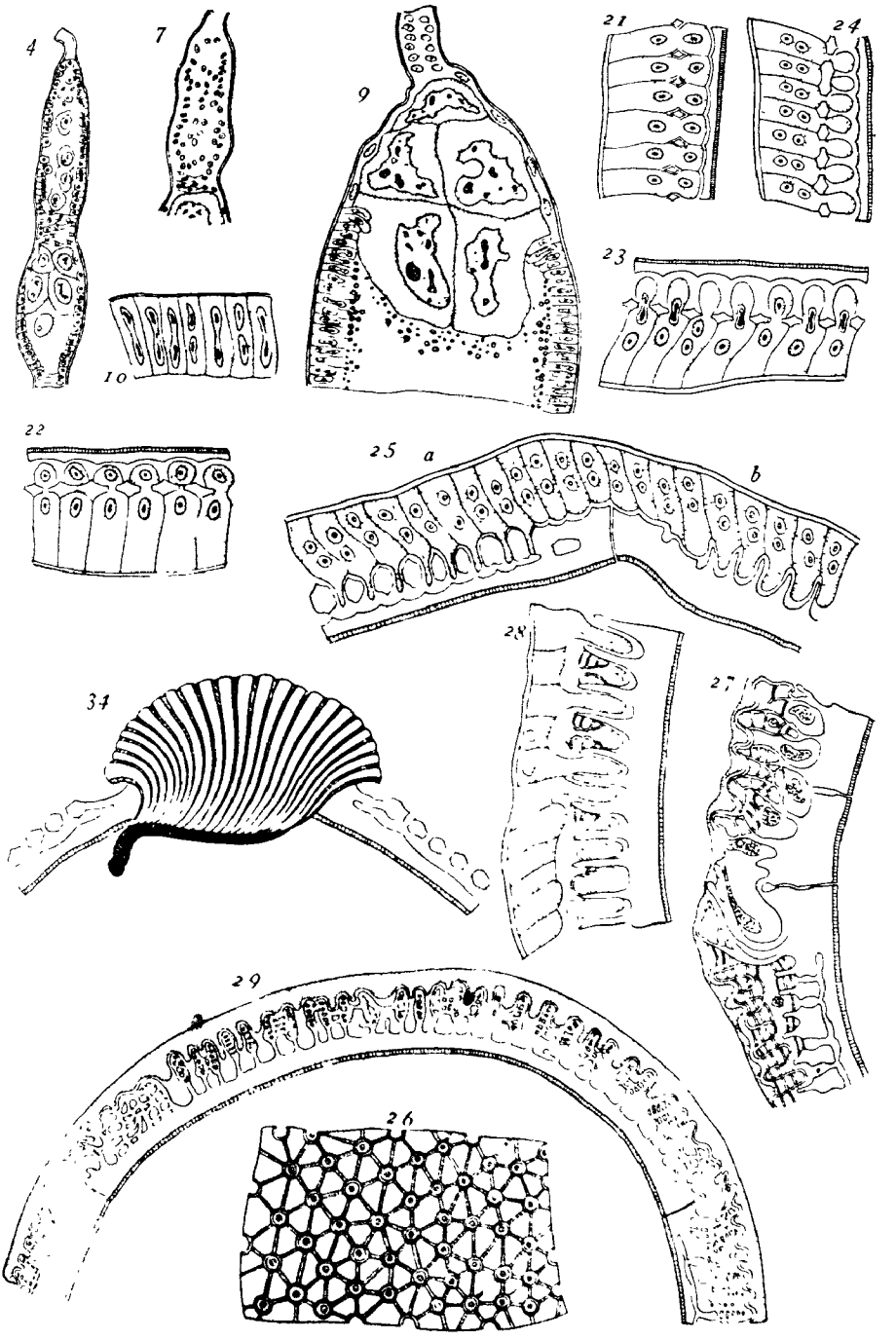
Plate LXVI

THE HOG LOUSE, HAEMATOPINUS SUIS LINNÉ

1, Longitudinal section through terminal chamber. 7, longitudinal section through terminal chamber 9, longitudinal section through egg chamber. 10, cross section through follicle cells, 24–25, cross sections through follicle cells in different stages in formation of epichorion. 26, surface view of epichorion. 27 and 28 cross section through follicle cells in different stages in formation of epichorion, 29, section through egg cap 34, longitudinal section through egg stigma

(Figures on this plate copied from Gross and numbered according to his arrangement)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CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

STUDIES IN POLLEN, WITH SPECIAL REFERENCE TO LONGEVITY

H. E. KNOWLTON

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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Altho much work has been done on problems concerned with pollination and fertilization, very little has been revealed as to the biology of the pollen itself. It is well known that the duration of viability of pollen varies with the species. It is found that corn and barley pollen only a few days old are unable to bring about fertilization, while date pollen may still effect fertilization after several years storage. The work done hitherto on this problem has consisted, for the most part, of mere observations, with no study of the underlying causes of pollen longevity. Aside from its scientific interest, the practical aspect of the question is important. The viability of pollen and practical methods of prolonging its life are of great importance to the plant breeder. With a knowledge of the most favorable conditions for pollen storage, it would be possible to cross plants blooming at different periods or those blooming in different parts of the world. This would permit more extensive crossing and a wider scope for the work of plant improvement.

The present work is a study of pollen and pollen longevity, with an attempt to determine, under different storage conditions, some of the reasons for pollen mortality. An endeavor was also made to discover practical methods of pollen storage.

EXTENT OF STUDIES

For a number of reasons, but particularly because it gave a fairly large quantity of pollen and a succession of blooms, snapdragon (*Antirrhinum majus* L.) was the chief material used in these experiments. The plants were grown in the greenhouse. For a short-lived pollen, corn (*Zea Mays* L.) was chosen. Some work was also done with apple (*Pyrus malus* L.).

Since the longevity of pollen was the primary interest, only those morphological and physiological studies were made which seemed to have a direct bearing on this problem. Extensive germination tests were made,

As a rule, light has no effect on germination, altho Sandsten (1910) found that with tomato pollen it was increased 25 to 50 per cent in sunshine. This increase, however, may be due to temperature effect.

Without doubt, the rôle of osmotic pressure in pollen germination has been overemphasized. Martin (1913) has attempted to determine the osmotic pressure of pollen grains. By means of the plasmolytic method, using different concentrations of cane sugar, he found the osmotic pressure of pollen of *Trifolium pratense* to be 165 atmospheres. His data show, however, that equivalent concentrations of different sugars produce widely different effects. He explains this on the basis of differences in the permeability of the sugars. Lloyd (1916, 1917) has presented data to show that, in the pollen of the sweet pea, it is the colloids of the grain that are more important. He concluded that "the living protoplasm as such behaves towards acids and alkalis in a manner sufficiently like that of gelatine to warrant the view that imbibition is a factor in growth." Osmotic factors are probably important in those species of pollen which do not germinate over a wide concentration of medium, as, for example, in the Graminae.

Duration of stigma receptivity

Horticulturists and investigators have generally assumed that a stigma is receptive from about the time the flower opens until the petals fall. As far as could be determined, there is no experimental evidence for this. Dorsey (1919) finds that in the native species of plum, the stigma, under normal conditions, remains receptive for about a week, but begins to turn brown after from three to five days. The styles begin to abscise about two weeks after blooming, but the abscission layer becomes very distinct in some varieties after eight days. Dorsey believes it doubtful whether the pollen tube is able to pass this abscission layer, for if pollination occurs late in the receptive period, only favorable growing conditions will allow the tube to pass the abscission layer before the style drops. As the petals fall from three to four days after blooming, it would seem that the duration of stigma receptivity is longer than that of the bloom. Undoubtedly, however, little pollination occurs after the petals have fallen, for bees seldom visit such flowers.

Anthony and Harlan (1920) worked on the period of receptivity of barley stigmas. In these investigations, flowers were pollinated each

day for six days. The percentage of fertilizations increased for two days, but from this time there was a gradual decrease until, on the sixth day, no pollinations brought about fertilization.

Pollen longevity

A considerable number of observations have been made by various workers on the life duration of pollen. However, as far as can be found, few carefully controlled experiments have yet been conducted.

The earliest reference to pollen longevity is in regard to date pollen. Kämpfer (1712) states that, if kept in a dark place, it is capable of fertilization the following year. Swingle (1904) writes that the Arabs make a practice of conserving, for use in the following year, a few bunches of staminate flowers, which are put in tight paper bags and kept in a dry, cool place. Bastin (1910) asserts that there is a tradition that date pollen will remain viable for fifteen years or even longer.

Gleditsch (1751) and Koelreuter (1797) state that the pollen of *Chamaerops humilis* will live for several weeks. The conditions under which the pollen should be stored are not stated, however.

Gärtner (1844) was successful in shipping the pollen of cycads, palms, and orchids. The longevity of many species varied from one to nine days. Gärtner found no relation between longevity of pollen and length of receptivity period of stigma.

According to Mangin (1886), the duration of life of the pollen of twenty different species of plants varied with the species; and among these the pollen of *Oxalis acetosella* lived for only one day, while that of *Picea excelsa* lived for eighty days, and that of *Antirrhinum majus* for forty-three days. The conditions of storage were not stated.

Sandsten (1910) found that the vitality of pollen was little affected by temperatures ranging from 25° to 55° C. in a dry atmosphere. A saturated atmosphere was injurious. Apple pollen was still alive after six months storage in a dry place at a temperature of from 8° to 26° C.

Molisch (1893) stored different species of pollen in watch glasses at room temperature and humidity. Longevity of pollen varied from two to six weeks, depending on the species.

Pfundt (1910) has done extensive work on the effect of moisture on pollen longevity. Pollen from one hundred and forty species of plants was subjected to different percentages of moisture at a temperature

ranging from 17° to 21° C., in darkness. Altho there were some exceptions, the duration of life was longest at 30 per cent humidity or in a perfectly dry atmosphere. Some of his data are given in table 1:

TABLE 1. SOME OF THE RESULTS OF PFUNDT'S INVESTIGATIONS OF THE EFFECT OF MOISTURE ON POLLEN LONGEVITY

Species	Per cent of moisture			Over H_2SO_4
	90	60	30	
Aesculus hippocastanum	6 days	17 days	72 days	72 days
Alisma plantago	1	1	1	1
Alnus glutinosa	32	46	59	53
Ampelopsis quinquefolia	6	11	23	19
Aquilegia vulgaris	5	14	84	92
Clematis integrifolia	6	24	89	103
Cornus mas	31	59	74	59
Corylus Avellana				65
Digitalis purpurea	9	13	43	172
Hippuris vulgaris	5	5	3–5	2
Impatiens Sultani	13	3	29	23
Lilium bulbiferum	8	31	142	142
Melilotus alba	6	14	96	73
Mercurialis perennis	8–10	29	58	72
Oenothera biennis	2	6	8	6
Pandanus furcatus	11	30	92	92
Papaver hybridum	33	17	49	49
Pinus montana				272
Pinus sylvestris				270
Pyrus malus				70
Plantago media	3	12	50	68
Poa compressa	1	1	1	1
Potentilla argentea	2	5	21	11
Prunus cerasus acida				81
Prunus padus	14	22	181	181
Salix alba				57
Salix gracilis	12	18	38	52
Secale cereale	12 hours	12 hours	12 hours	12 hours
Solanum dulcamara	7 days	9 days	11 days	11 days
Tradescantia Virginica	2	3	31	10
Tulipa Gesneriana	23	43	108	92
Ulmus campestris	6	9	22	17
Viburnum opulus				164
Vicia faba				21
Viola odorata	19	28	217	235

Crandall (1913), storing pollen in covered petri dishes, found that apple pollen one month old would not germinate, but that when eleven days old it was still capable of fertilization. Strawberry pollen three

hundred and seventy-seven hours old, fertilized successfully, and sweet-pea pollen fertilized after twenty-three days.

Kellerman (1915) shipped Citrus pollen from Florida to Japan, using four methods of storage: (1) in cork-stoppered vials, (2) in cotton-stoppered vials, (3) anthers in glass tubes exhausted to 10 millimeters pressure, and (4) anthers in dried glass tubes exhausted to 0.5 millimeter pressure. During shipment, which covered a period of from four to six weeks, the pollen was kept at a temperature as near 10° C. as possible. Both the third and fourth methods were successful, but the fourth was the more so.

Andronescu (1915) worked on the longevity of corn pollen. Corn pollen kept in a dry oven, at 42° C., was killed in twenty minutes, while in a saturated atmosphere, under the same conditions, there was 32 per cent of germination. Pollen exposed in the laboratory died in two hours; uncovered, out of doors, it lived for four hours; in 60-per-cent moisture, for six hours; in 90-per-cent moisture, for forty-eight hours Pollen in sealed tubes lived for twenty-four hours.

McClure (1892), also working with corn pollen, found that if kept dry it retained its vitality for several days.

Roemer (1915) stored pollen both in cotton-stoppered test tubes and in gelatine capsules. He concluded that pollen remained viable longest under low temperature (5°–10° C.) and low moisture conditions.

Tokugawa (1914), using species of Lycoris, Torenia, and Narcissus, and Simon (1911), using pumpkin, also found that the pollen lived longest in a dry atmosphere. The pumpkin pollen lived for five weeks in a sealed vessel containing anhydrous calcium chloride. Adams (1916) found that, in a dry condition, apple pollen kept for three months; pear pollen, for ten weeks. Strawberry, loganberry, and raspberry pollen were dead after two months and black-currant pollen was dead after eleven weeks.

Horsford (1918) preserved pollen of *Lilium auratum* until the following spring by wrapping it in several sheets of paraffin paper and storing it in a warm, dry place. It rapidly lost its vitality on exposure to air.

Anthony and Harlan (1920) worked with barley pollen. They used both artificial methods of germination, and germination directly on the stigma, as tests of viability. Pollen twenty-four hours old produced a greatly decreased percentage of fertilization, while pollen forty-eight hours old was incapable of effecting fertilization. Pollen stored under conditions which retarded evaporation remained viable for the longest time.

It is evident, from a study of these experiments, that the pollen of most species remains viable longest under conditions of low temperature. Altho there are few available data, the indications are that the optimum moisture conditions vary with the species.

In all of the experiments mentioned in the foregoing paragraphs, artificial germination, except as otherwise noted, was the only test of viability used in the investigations. As will be shown by the author's experiments, this is not always a proof of ability to bring about fertilization.

Possible causes of death of pollen

As far as the writer has learned, Andronescu (1915) is the only investigator who has advanced a theory to explain the cause of death of pollen. He found that corn pollen stored out of doors lost 48 per cent of its moisture in two hours and 52 per cent in twenty-four hours. Since he found also that pollen lived longer at higher humidities, he concluded that death is the result of desiccation. Pfundt (1910), however, determined that the range of moisture required is wide, depending on the species: some live longer at low, others at high humidities. It is not possible to conclude, therefore, that desiccation is always the cause of death.

Investigators generally agree that the duration of life is longer at fairly low temperatures. This is to be expected, as physiological activities are slower.

Altho pollen and seeds differ morphologically as well as in function, it was thought that the cause of death in each might be similar. A brief discussion of the causes of death in seeds is, therefore, desirable.

Acton (1893) found that thirty-years-old wheat which had lost its germinative power, contained about the same amount of stored food but less water than did new grains, and that its amylase and proteolytic enzymes had also been destroyed. On the contrary, Brocq-Rousseu and Gain (1909) state that amylase and oxidase were present in wheat grains ranging from twenty-five to eighty years old. White (1909) states that amylase was present in fairly large quantities in old seed of wheat, barley, oats, rye, and corn. The age of the seeds tested ranged from two to twenty-one years. The addition of amylase did not cause dead seeds to germinate.

Crocker and Harrington (1918) and their coworkers found that, in some seeds, catalase activity is correlated with physiological activity and

decreases with age. Crocker and Groves (1915) advance a theory that the loss of viability of seeds in storage is due to a slow coagulation of the proteins in the plasma of the embryo. They applied Buglia's (1909) time-temperature formula for protein coagulation and found it applicable for a temperature-life-duration formula for seeds. This formula is

$$T = (a-b) \log Z$$

in which T represents the temperature and Z the time of heating, and a and b are constants. Several factors, such as the increase in acidity of the seed, the redispersal of proteins in seeds of high water content, and variability in the water content, may limit the general application of this formula. A slight error in a and b gives a relatively large error for a life duration at low temperatures.

There are no records of attempts to determine whether the death of pollen is due to any of these causes, that is, exhaustion of stored food, destruction of enzymes, or coagulation of proteins.

EXPERIMENTAL WORK

Description of pollen

Pollen of snapdragon (Antirrhinum majus L.)

The pollen of snapdragon is produced very abundantly. It is yellow in color and is covered with a gummy substance which causes the grains to adhere to one another. As this sticky pollen cannot be wind-carried, cross-pollination is effected by bees and other insects. The pollen is rather below the average in size; is oval in shape, when dry, but when turgid, in a sugar solution, is nearly spherical. Dry pollen measures 26.5μ in length, and 15.3μ in width; when turgid, the average diameter is 24μ. Halsted (1889) has noted a similar change in shape with other species of pollen. When dry, the position of the germ pores is marked by three long folds in the wall. These folds are less distinct when the cell becomes turgid.

Analyses of fresh pollen show that cane sugar is the reserve carbohydrate, the amount present, expressed in percentage of fresh substance, varying from 8 to 10 per cent. Small amounts of reducing sugars are also present, but no starch was detected.

Other investigators have made chemical analyses of pollen. Van Tieghem (1869) observed that some species of pollen store cane sugar.

Von Planta (1885) found 14 per cent of cane sugar in Corylus pollen and 11 per cent in Pinus pollen. Mangin (1886) noted that Betula and certain Coniferae pollens have reserve starch, while others (Narcissus) have stored sugar only. Green (1894) stated that many species of pollen contain starch, glucose, maltose, and cane sugar. In the immature pollen grains of wheat, Eckerson (1917) at first found glucose, and later, starch appeared. Martin and Yocum (1918) state that, at pollination time, apple pollen contains proteins and small amounts of sugar. According to Green (1894) and others, these organic reserves are broken down by appropriate enzymes during the germination of the pollen.

Determinations show a surprisingly small water content, only 10 to 20 per cent being present. The amount varies under different conditions and in different seasons.

Pollen of corn (Zea Mays L.)

Corn pollen is produced in large quantities. This fact was one of the reasons for its selection as a material for testing in these experiments. Under favorable conditions, in the early morning, it was very easy to collect from 25 to 30 grams of pollen in a cornfield. This allowed analyses to be made, which could not have been done with the more scanty pollen of other species. Corn pollen seems very dry, does not adhere, and is consequently wind-borne.

Fresh corn pollen is oval to round in shape, altho elongated grains are often noticed. On exposure, they become shrunken. Corn pollen is larger than Antirrhinum, measuring 106μ by 120μ. When the microscope is properly focused, circular germ pores, one to three in number, can be seen. These pores resemble bordered pits of wood tissue.

Unlike Antirrhinum pollen, starch is the storage carbohydrate of corn pollen, whole pollen grains often staining a deep blue in iodine solution. Other grains did not stain so deeply, indicating that they contained less starch. Chemical analyses showed about 10 to 15 per cent starch, expressed in percentage of fresh substance. The table given by Andronescu (1915) shows 39 per cent of total carbohydrates. No starch analyses were made by him.

Altho corn pollen is wind-borne and seemingly dry, the moisture content is very high. Determinations made by the writer showed that it ranged from 50 to 65 per cent, depending on the amount of moisture in the air,

the maturity of the tassel, and the amount of water available to the plant. In illustration of this, pollen freshly gathered in the field showed 52 per cent of water, while pollen gathered in the laboratory, from tassels standing in a jar of water, contained 63 per cent of moisture. Andronescu (1915) states that corn pollen has an average moisture content of about 57 per cent. As will be shown later, it loses moisture rapidly on exposure to conditions of low humidity.

Method of pollen germination

In all artificial germinations the following method was used: A small quantity of pollen was placed in a drop of sugar solution or sugar-agar solution, on a cover glass. The cover glass was then inverted over a Van Tieghem cell which contained several drops of the same solution. Vaseline was placed around the edges of the cell to secure the cover glass and to prevent evaporation

Germination of Antirrhinum pollen

Antirrhinum pollen germinated well in a cane-sugar solution, very high percentages of germination resulting. There was no very great sensitiveness as to concentration. At one time the highest percentage of germination would result at one concentration, at other times, at another. In general, the best germination was obtained in a 15- to 25-per-cent cane-sugar solution. There was a small percentage of germination in water. The range of concentration at which germination occurred is shown in table 2. In other experiments a higher percentage of germination, even as high as 80 to 90 per cent, was obtained.

TABLE 2. GERMINATION OF ANTIRRHINUM POLLEN

Cane-sugar (per cent)	5	10	15	20	25	30
Germination (per cent)	38	18	42	70	32	3

As the germ-tube growth progressed, a thickening of the tube wall occurred at several points back of the growing tip. These areas increased in thickness until finally the whole tube was plugged with callose. These callose plugs can be seen in unstained slides, but a short immersion in

a weak aniline-blue solution brings them out more clearly. In pollen tubes of apple, the plugs are more numerous than in Antirrhinum.

The germination of Antirrhinum pollen was greatly stimulated by the addition of a minute amount of the crushed stigma of Antirrhinum. Pollen in a sugar solution showed germ tubes appearing after one and one-half hours. The addition of a piece of the stigma to the same concentration of sugar so stimulated germination that within one hour the germ tubes were from one to four times the diameter of the grains in length. Marked chemotropism also resulted, the germ tubes growing toward, and even penetrating, the stigma tissue. No effect was obtained by the addition of either geranium or petunia stigmas, however.

Even pollen from anthers that had not dehisced was germinated. Pollen from anthers which would have dehisced three days later showed no germination after two hours, in contrast to mature pollen, which showed a 60-per-cent germination. After twenty hours, the immature pollen showed a 65-per-cent germination, while the mature pollen gave an 85-per-cent germination. The germ tubes of the mature pollen were longer. A small percentage of germination was obtained with more immature pollen, but it was very slow and weak. Very immature grains, below normal in size, seemed to grow larger when placed in a nutrient solution, but no germination took place. It is apparent, then, that pollen matures several days before the anthers dehisce.

Optimum temperatures for Antirrhinum-pollen germination were determined. The pollen was taken from the same anther. The results, given in table 3, are the averages of six cultures for each temperature, the media being cane-sugar solutions:

TABLE 3. ANTIRRHINUM POLLEN GERMINATION AT DIFFERENT TEMPERATURES

Temperature (centigrade)	21°	26°	29°	33°
Germination (per cent)	36	56	22	15

Under the conditions of the experiment, it may be concluded that the optimum temperature for the germination of Antirrhinum pollen is about 25° C.

Germination of corn pollen

Great difficulty was experienced in the first attempts to germinate corn pollen. There was no germination in water, altho Jost (1905) claims to have succeeded in obtaining it. Various kinds and concentrations of sugar were tried unsuccessfully. Pieces of stigma and decoctions of stigmas had no effect. Occasionally, several grains developed short germ tubes, but there was no general germination.

Later experiments were more successful. A 20-per-cent germination was obtained in 10-per-cent cane sugar plus 0.7-per-cent agar, as recommended by Andronescu (1915). By varying the concentration, even better germination resulted, as is shown in table 4:

TABLE 4. GERMINATION OF CORN POLLEN

Medium		Germination
Agar +	Cane sugar	
Per cent	*Per cent*	*Per cent*
1 0	15 0	56
0 7	15 0	62
0 7	20 0	18
0 5	17 5	30
0 5	15 0	3

Germination is so rapid that after two or three minutes the protrusion of the tubes may be observed. The subsequent elongation was slower. Protoplasmic streaming was plainly visible in the germ tubes. After twenty-four hours, the germ tubes ranged in length from one to seven times the diameter of the grains.

Good germination was not obtained consistently. At times, the results from a certain concentration of solution were excellent; again, the same strength of solution failed to induce germination. Apparently the water relations were very delicate and the concentration had to be exactly correct before germination could take place. This is a common difficulty with the pollen of Graminae, according to other investigators (Anthony and Harlan, 1920). Martin (1913) found this to be true also of the pollen of *Trifolium pratense*.

As the water content of corn pollen is high, it is probable that osmotic pressure plays an important part, both in the swelling of the grain and in its subsequent growth. This idea is strengthened by the fact that a definite concentration of sugar is necessary, any departure from which results in failure to germinate or in abnormal germination. It is difficult to understand why a definite concentration would be necessary if colloidal imbibition played the main rôle. On the other hand, the water content of Antirrhinum pollen is low and the pollen germinates in almost any concentration of sugar. Imbibition is probably more important here than is osmosis.

Results were so variable that it was thought best not to use artificial germination as a test of viability in the experiments on longevity of corn pollen. Only fertilization tests were employed, therefore.

Apple (*Pyrus malus* L.) pollen resembles Antirrhinum pollen in that it is easy to germinate and is not sensitive as to the concentration of sugar solution, as is indicated in table 5.

TABLE 5. GERMINATION OF APPLE POLLEN (25° C.)

Sugar solution	Germination	Length of pollen tubes *
Per cent	*Per cent*	
2 5	1	Short
5 0	2	Short long
7 0	3	Short medium
10 0	12	Short medium
12 0	15	Short long
15 0	30	Short long
17 0	30	Short long
20 0	20	Short medium
22 0	7	Short
25 0	30	Short medium
28 0	30	Short medium
30 0	25	Short long

* Short signifies a length of from 1 to 5 pollen-grain diameters; medium, a length of from 5 to 10 pollen grain diameters; and long, a length of from 10 to 25 pollen grain diameters.

Altho Knight (1918) found that the addition of pieces of the stigma to the medium exerted no favorable action, the author thus procured stimulation repeatedly, and even chemotropism. It was not as pronounced as with Antirrhinum pollen, however.

Duration of receptivity of the stigmas of Antirrhinum

In any pollination experiment, data concerning the duration of stigma receptivity are important. Few investigators of pollination problems study this phase of the work, however. As has been mentioned, Dorsey (1919) determined this period for the plum, and Anthony and Harlan (1920) for barley.

In order to find out the length of time stigmas of Antirrhinum remain receptive, the following experiment was conducted. A large number of flowers were emasculated prior to the time the petals unfolded, and pollinations with fresh pollen were made at intervals up to several weeks after the opening period of the flowers. Results of this experiment are given in table 6:

TABLE 6. DURATION OF RECEPTIVITY OF ANTIRRHINUM STIGMAS

Day after flowers opened	Number pollinated	Number fertilized	Number not fertilized
Same day	11	9	2
5th	6	6	0
6th.	6	6	0
8th.	8	8	0
10th.	11	10	1
14th	7	1	6
16th	5	3	2
18th	4	0	4
21st.	11	2	9
23d.	5	0	5
25th.	5	0	5

Two weeks after pollination, capsules were produced, but these were smaller and contained a smaller number of seeds. The pistils of emasculated flowers, if the pollen was withheld for any length of time, grew to an abnormal size. After from fifteen to eighteen days, the pistils began to wither.

These results show that after ten days the percentage of fertilization decreased, altho several fertilizations took place on flowers three weeks old.

The duration of receptivity of corn stigmas was not determined. It is generally understood by plant breeders, however, that corn can be pollinated successfully until the silks begin to wither.

Storage experiments with Antirrhinum pollen

Influence of temperature

The investigation of pollen storage, in 1915, consisted only of a study of the effect of different temperatures on pollen longevity. Both the germinative power on artificial media and the ability to actually fertilize

TABLE 7. ANTIRRHINUM POLLEN STORED AT 40° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
0			60	15	
3	1	1	80	20	
5	2	0	42	30	Short
10	5	1	54	25	Short
14	5	0	47	30	Short
21	3	0	65	20	Short-medium
28	7	1	60	25	Short medium
42	3	0	30	20	Short

TABLE 8. ANTIRRHINUM POLLEN STORED AT 30° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	3	3			
5	6	2	35	25	Short medium
10	3	0	2	25	Short
14	6	4	0		
21	5	0	0		
28	3	0	0		

TABLE 9. ANTIRRHINUM POLLEN STORED AT 21° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	4	3	32	10	Short-long
5	7	4			
10	1	1	13	15	Short-medium
14	6	1	8	20	Short-medium
21	3	2	9	15	Short
28	4	1	27	25	Short
42	4	0			

TABLE 10. ANTIRRHINUM POLLEN STORED AT 0° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	7	5	9	15	Short-medium
5	7	4	40	25	Medium-long
10	4	4	72	20	Medium-long
14	3	2			
21	9	2	56	20	Short-long
42	6	2	12	25	Short
88			0		

were used as tests of viability. Since concentrations in which maximum germination took place varied on successive days and with different samples of pollen, six concentrations of cane sugar were used for each test. Slides were examined after twenty-four hours. Pollen was stored in small stoppered bottles, one for each withdrawal.

TABLE 11. ANTIRRHINUM POLLEN STORED AT −18° TO −30° C. 1915

Age	Flowers pollinated	Seed capsules developed	Greatest germination	Sugar concentration in which maximum germination resulted	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	*Per cent*	
3	3	2	20	30	Short
5	8	2	47	20	Short-long
10	10	9	50	10	Short-long
14	6	4	35	25	Long
21	6	0	12	25	Short-medium
28	3	0	36	15	Short-long
42	3	1	20	20	Short-medium
88			26	30	

TABLE 12. ANTIRRHINUM POLLEN STORED AT −18° TO −30° C. 1917

Age	Flowers pollinated	Flowers fertilized	Germination	Average length of pollen tubes
Days	*Number*	*Number*	*Per cent*	
7	6	6	30	Long
28	8	5	50	Short-long
42	10	10	60	Medium long
77	5	5	60	Medium long
105	6	4	50	Short-long
133	5	4	50	Short-long
161	5	3	50	Short-long
189			15	Short-medium
217			1	Short

In the 1917 experiment, pollen was still capable of fertilizing after storage for 161 days at −18° C. to −30° C. No other temperature experiments were performed that year.

These results show an increasing longevity as the temperature at which pollen was stored decreased. At 40° C., only three fertilizations resulted and artificial germinations showed a weak pollen-tube growth. At 30° C. there were more fertilizations, but germination was poorer. Storage conditions were more favorable at 21° C. At this temperature, the pollen

was still capable of fertilization after one month. Germination grew progressively weaker with increasing age. At 0° C., pollen remained viable for six weeks. Germination was better and pollen tubes grew longer than when stored at other temperatures. The pollen had not lost its germinative power after three months at −17° C. to −30° C. It may be concluded, therefore, that the lower the storage temperature, the longer Antirrhinum pollen remains viable.

These experiments also show that the optimum sugar concentration for artificial germination varies from 10 to 30 per cent.

Influence of carbon dioxide

Since Kidd (1917) had found that high percentages of carbon dioxide in the atmosphere depressed the respiration of the seeds and therefore increased the period of longevity, some pollen-storage experiments were made under these conditions in 1917. Sealed glass tubes containing 15 per cent of carbon dioxide were used as receptacles.

The results, tho inconclusive, seemed to show that Antirrhinum pollen will remain viable longer in an atmosphere containing 15 per cent of carbon dioxide than in normal air. Similar conditions will result, however, whenever pollen is stored in containers merely sealed, for, due to respiration, the carbon dioxide content of the inclosed atmosphere will increase.

In 1917, some pollen was stored in pure carbon dioxide. Sealed glass tubes were again used as containers. The results are given in table 13:

TABLE 13. ANTIRRHINUM POLLEN STORED IN PURE CARBON DIOXIDE AT 10–20° C. 1917

Age	Pollinated		Fertilized		Germination		Average length of pollen tubes	
	In air	In carbon dioxide	In air	In carbon dioxide	In air	In carbon dioxide	In air	In carbon dioxide
Days	*Number*	*Number*	*Number*	*Number*	*Per cent*	*Per cent*		
7	5	9	5	6	50	60	Short	Medium–long
21	12	15	10	9	20	60	Short–medium	Medium
28		15		11	60	40	Medium long	Medium
42	4	7	3	6	60	60	Medium long	Short–medium
49		7		4		60		Medium
63		10		9		10		Short–medium
86		6		1		25		Short medium
105	8	4	4	4	40	50	Medium	Short long
121	6	8	6	8				

Pollen remained viable for four months in an atmosphere of carbon dioxide. In this atmosphere, the small amounts of respiration that occurred must have been anaerobic. Kidd (1917), however, has shown that carbon dioxide has a retarding effect on both aerobic and anaerobic respiration.

Influence of reduced pressure

Kellerman (1915) found that Citrus pollen remained viable longer under low atmospheric pressures. Some experiments were made in 1917 to determine whether this was true also with Antirrhinum pollen. The pollen was stored in sealed glass tubes, with the atmospheric pressure reduced to 100 millimeters.

TABLE 14. ANTIRRHINUM POLLEN STORAGE AT A PRESSURE OF 100 MILLIMETERS COMPARED TO STORAGE AT NORMAL ATMOSPHERIC PRESSURE, AT 0° C. 1917

Age	Flowers pollinated		Seed capsules developed		Greatest germination		Average length of pollen tubes	
	In normal pressure	In reduced pressure	In normal pressure	In reduced pressure	In normal pressure	In reduced pressure	In normal pressure	In reduced pressure
Days	*Number*	*Number*	*Number*	*Number*	*Percent*	*Percent*		
7	8	0	8	8	15	15	Short long	Medium long
25		0		7	10	60	Medium long	Medium long
42	13	3	12	3	50	10	Medium long	Medium long
77	8	2	8	2	70	15	Medium long	Short medium
105	5	6	2	3	60	0	Medium long	
133	4		4		60	0	Medium long	
161	8		8		50		Short medium	

Under normal atmospheric pressure, pollen remained viable longer than under reduced atmospheric pressure. Another series, at 10° C., gave similar results. Dade (1903) also found this to be true with certain kinds of seeds. He attributed the lessening of longevity to the injurious products formed in anaerobic respiration.

Influence of storage in pure oxygen

Storage in oxygen was studied in 1917, with results as shown in table 15. The pollen was stored in sealed glass tubes.

Due to the absence of the author during the war, no tests were made from the 196th day to the 670th day. Altho there was weak germination after the long storage, it is significant that there were no fertilizations. Undoubtedly, respiration was more active; perhaps, also, there was an

exhaustion of stored food. Since more favorable results were obtained in normal air than in pure oxygen, it would appear that normal atmosphere is more favorable to the prolongation of viability.

TABLE 15. ANTIRRHINUM POLLEN STORAGE IN PURE OXYGEN COMPARED TO STORAGE IN AIR (19°–22° C.). 1917

Age	Flowers pollinated		Seed capsules developed		Percentage of germination		Average length of pollen tubes	
	In air	In oxygen	In air	In oxygen	In air	In oxygen	In air	In oxygen
Days	*Number*	*Number*	*Number*	*Number*	*Per cent*	*Per cent*		
7	9	3	8	3	70	65	Medium-long	Long
14					50		Long	
28		6		5		40		Medium-long
35	7		6		40		Short long	
42		6		5		60		Medium-long
56	12		11		40		Medium long	
98		5		3		40		Medium long
112	4		1		60		Medium-long	
126		6		2		30		Medium-long
140	2		2		60		Short long	
172		5		2		30		Short-long
196			0		5		Short	
181						10		Short-medium
1.5			0		0			
650	8		0		50*	10*	Short-medium	Short.

*Pieces of stigma added. No germination occurred in absence of stigma.

From the results of all these storage experiments, it may be concluded that Antirrhinum pollen remains viable longest at low temperatures. Moisture conditions, provided they are not too high, are not important. Storage under low atmospheric pressures does not yield good results. Pollen remains viable longer in normal atmosphere than in pure oxygen. There is some evidence that an atmosphere of pure carbon dioxide or one containing large percentages of it favors longevity. The results obtained in 1917 were better than in previous years, a fact which may be due, in part, to the sealed glass tubes used as storage containers, but which is more probably due to the greater virility of the pollen produced in 1917. The author wishes to emphasize the fact, mentioned by other investigators (Kellerman, 1915), that pollen varies greatly. Many data had to be discarded because of this uncontrollable factor.

The writer has demonstrated that Antirrhinum pollen can be stored a longer time than forty-three days, which was the limit reported by

Mangin (1886). If the temperature remains low, Antirrhinum pollen should remain viable for five months or longer, tho the variability of pollen may necessitate a qualification of this statement.

Possible causes of death of Antirrhinum pollen

Loss of moisture

As Antirrhinum pollen has a low water content, it was believed that moisture conditions would not affect longevity to any great extent. Under very humid conditions, however, moisture collected on the pollen and contaminations by molds soon resulted.

To determine whether the Antirrhinum pollen would lose moisture rapidly, a small quantity of pollen was spread on a watch glass, weighed, and placed in the incubator at 25° C., where the humidity ranged from 20 to 40 per cent. Weighings were made daily. At the end of seventy days the weight was practically the same as at the beginning. Slight fluctuations occurred during this period, as the humidity within the chamber varied. Since little moisture loss occurred, this sample of Antirrhinum pollen must have been in equilibrium with the atmosphere at this particular humidity. The fact that the pollen had lost little water, altho exposed for seventy days to an atmosphere low in humidity, would indicate that moisture loss does not condition the duration of viability.

Respiration experiment

Exhaustion of the stored carbohydrates suggested itself as a cause of death. Since the water content is low, metabolic processes, and particularly respiration, should be less active. To determine the truth of this, an attempt was made to study respiration. Several methods were tried, but none were successful because the amount of carbon dioxide given off was so very small. Difficulties were enhanced by the necessarily small amounts of material. The conclusion drawn from these attempts was that the respiration rate of Antirrhinum pollen is very low — probably comparable to that of seeds having a low moisture content.

Depletion of cane sugar

Altho respiration seemed a negligible factor, it was deemed advisable to make carbohydrate analyses of fresh and stored pollen, in order to

determine whether there was any diminution. Sachsse's method was used. Pollen was stored at room temperature in sealed bottles. The results are given in table 16:

TABLE 16. CARBOHYDRATE ANALYSES OF ANTIRRHINUM POLLEN

Age	Condition	Percentage of fresh substance	
		Reducing sugar	Sucrose
Days		*Per cent*	*Per cent*
0	Alive	0 40	7 20
11	Alive	0 55	6 80
240	Dead	3 90	1 20
310	Dead	2 10	0 32

These results show a perceptible decrease in the stored sugars as the age of pollen increases, this reserve probably having been used in respiration. As the dead pollen still contained a large amount of stored food, it is improbable that a lack of it had caused the mortality.

Decrease of certain enzymes

Since cane sugar is the chief storage carbohydrate, invertase would be one of the important enzymes present. Tests were therefore made of the activity of invertase as the age of the pollen increased. Weighed quantities (100 milligrams) of Antirrhinum pollen were placed in small bottles at room temperatures. At the intervals given in table 17, invertase was extracted and a determination of its activity was made. The method used was similar to the one recommended by Green (1894). The pollen (100 milligrams) was ground for several minutes in a mortar with a few drops of a 5-per-cent sodium-chloride solution. It was then diluted to 10 cubic centimeters and filtered. To 10 cubic centimeters of 5-per-cent cane-sugar solution was added 2 cubic centimeters of this extract. Digestion continued for twenty-four hours at 30° C. The results are given in table 17.

These results indicate a marked decrease in the invertase content in dead pollen over that in live pollen. However, there is still some invertase present.

TABLE 17. INVERTASE ACTIVITY OF ANTIRRHINUM POLLEN

Age of pollen	Invert sugar	Condition of pollen
Days	*Milligrams*	
0	189 7	Alive
30	195 6	Alive
270	7 7	Dead
570	15 8	Dead

An increase in the proportion of reducing sugar as the age of the pollen increases is shown in table 16. There are several possible explanations of this. A decrease in respiration would tend to result in a surplus of reducing sugar, provided that invertase activity continued at the same rate. In other words, this respiratory material would not be used as rapidly as it would be formed. There may also be a readjustment in the cell protoplasm which would bring more of the enzymes in contact with the cane sugar. As metabolic activities proceed, this reorganization may very probably be taking place.

This suggests the theory of Crocker and Groves (1915) that the death of seeds is caused by a coagulation of the proteins of the protoplast. An attempt was made to apply the temperature-time-of-coagulation formula to loss of viability of Antirrhinum pollen. Consistent results could not be obtained, probably because the moisture content of the pollen grains varied. However, it was found that Antirrhinum pollen can withstand high temperatures to a remarkable degree.

The activity of catalase was very great in fresh pollen. There was some activity in dead pollen, but the decrease over that of fresh pollen was noticeable.

Storage experiments with corn pollen

Since the results of previous workers pointed to the beneficial effects of low moisture conditions on pollen longevity, experiments were made with this in mind, in 1915. Sweet corn was used, the variety being Golden Bantam. Corn pollen for each series was mixed thoroly and stored, in paper envelopes, in covered glass fruit jars. The pollen was divided into several envelopes, for convenience in withdrawing parts of it at the end of each interval. Each jar had several inches of anhydrous

calcium chloride in the bottom. The receptacles were then placed in constant-temperature ovens, at the temperatures noted in tables 18, 19, and 20. At the end of each specified interval, an envelope was withdrawn from each jar, and with its contents field pollinations were made. After a suitable interval, the ears were examined to determine whether fertilization had occurred. Ability to fertilize was the only test of viability used, since uniform results could not be obtained in artificial germination experiments.

In table 18, fertilization is indicated by a plus sign, and lack of fertilization by a minus sign. The number of ears pollinated was either one, two, or three, as indicated by the number preceding the sign.

TABLE 18 CORN POLLEN STORED AT DIFFERENT TEMPERATURES OVER CALCIUM CHLORIDE 1915

Length of storage	Fertilization when stored at				
	−17° C.	0° C.	12° C.	22° C.	34° C.
Hours					
6			1+	1+	2—
12			1+		
22		1+	1+		
24	1		1+	2+	2—
30	1			1—	2—
32			1+		
36				2—	
45		1+	1+		
48	1				
51		1+			
54	1			3—	2—
60				2—	
72	1		1+		1—
78					1—
93		1+		1—	1—
99			1+		
120	1	1			
131		3			
179		3			
192	1				

These results point to the fact that moderately low temperatures are most favorable for storing corn pollen, provided the humidity is low. It should be noted that pollen stored at a temperature of −17° C. was not capable of effecting fertilization. In this series, no pollinations were made

until after twenty-four hours. There is no evidence as to the exact time at which the loss of fertilizing power occurred.

TABLE 19. CORN POLLEN STORED AT DIFFERENT TEMPERATURES AT A HUMIDITY OF 5–10 PER CENT. 1915

Length of storage	Pollen stored at							
	0° C.		10° C.		20° C.		30° C.	
	Ears pollinated	Fertilization	Ears pollinated	Fertilization	Ears pollinated	Fertilization	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
6	4	0	2	45	1	85	3	90
12	3	0	2	60	2	45		
15	4	0		20			2*	45
24	2	0	5	49	4	36	2	3
30	3	0	7	0	2	0	1	0
36					2	30		
48			3	0	6	0		
54			1	0	1	0		
60			3	0				
72			4	0				

* Pollen adhering

TABLE 20. CORN POLLEN STORED AT 80–90 PER CENT HUMIDITY AT TEMPERATURES OF 20° C. AND 30° C. 1915

	Length of storage	Ears pollinated	Fertilization
	Hours	*Number*	*Per cent*
Pollen stored at 20° C.	6	2	24
	24	2	67
	30	2	82
	36	2	53
	48	3	23
	54	1	0
Pollen stored at 30° C.	6	1	68
	15		
	24*	3	0
	30*	2	0

* Pollen adhering.

In the experiments conducted in the summer of 1916, pollen was subjected to different moisture, as well as different temperature, conditions. The pollen was stored in bottles. The several percentages of moisture were obtained by drawing air thru different concentrations of sulfuric acid, according to the tables of Landolt-Börnstein. Withdrawals and field pollinations were made as in the 1915 experiments. The percentage of fertilization was obtained by actually counting the fertilized and unfertilized ovules on each ear.

TABLE 21. CORN POLLEN STORED AT 30° C. AND 20–30 PER CENT HUMIDITY. 1916

Length of storage	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*
6	1	0
12	3	12
24	2	0
30	2	0

Other storage experiments were made, but temperature conditions at pollination time were so unfavorable that the results were discarded.

Under conditions of high humidity, moisture often collects on the pollen, causing the grains to swell and adhere to one another. On microscopic examination, films of water are seen around the grains. This water does not come from the air, but is excreted by the pollen grains themselves. This is shown by the fact that this "caked" pollen has not increased in weight. As individual pollen grains differ in the amount of colloids and in the concentration of osmotically active substances, it is possible that one grain extracts water from another. However, if this were true, one would expect some grains to be shrunken, which is not the case, so some other explanation must be found. Such changes as coagulation or precipitation of the proteins may take place within the protoplast, which would lessen its power to retain water. A secretion of water would then result. The caking of pollen impairs its viability and interferes with the mechanical operations of pollination. Caked pollen is also a favorable medium for the growth of molds and other fungi.

The results of these experiments again show the favorable effects of fairly low temperatures. A freezing temperature, however, seems to be injurious, and in this respect corn pollen differs from pollen of most species. When corn pollen does not adhere, high humidity seems to prolong its fertilizing power.

Only two storage experiments were conducted in 1917, owing to war conditions. The pollen was stored in watch glasses, over different percentages of sulfuric acid. Novy jars were used. The pollinations were made as in 1916. The results are given in table 22:

TABLE 22. CORN POLLEN STORED AT 6°-10° C. UNDER HUMIDITIES OF 50 PER CENT AND 80 PER CENT. 1917

Length of storage	Ears pollinated		Fertilization	
	50 per cent humidity	80 per cent humidity	50 per cent humidity	80 per cent humidity
Hours				
6	1	2	85	45
10	3	3	48	20
24	2	2	75	52
30	3	3	62	62
46		6		34
54		1		60
71	3	3	70	30

Pollen produced in 1917 was more virile than that of previous years and it is to be regretted that more experiments could not be made. Contrary to the results of the previous year, the lower humidity was the more favorable to longevity.

In order that atmospheric conditions might be more easily controlled, corn plants were grown in the greenhouse in 1919. As a result, favorable and uniform temperatures were maintained both day and night during pollination time, which was a great aid in getting comparable results.

As in previous seasons, actual fertilizing power was the only test of viability used. The method of storage of pollen was the same as in 1917.

The results from these experiments (tables 23, 24, 25) are not very conclusive, altho it can be seen that the pollen lived longer at the lower temperatures. The percentage of fertilization was smallest at the lowest

TABLE 23. CORN POLLEN STORED AT 14° C. AND 70 PER CENT HUMIDITY. 1919

Length of storage	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*
4	2	43
11	1	70
25	1	0
35	2	0
50	2	30
60	1	60
71	1	0
85	1	0
100	2	5
108	0	0
121	4	0

TABLE 24. CORN POLLEN STORED AT 25° C. AND 50 PER CENT HUMIDITY. 1919

Length of storage	Ears pollinated	Fertilization
Hours	*Number*	*Per cent*
5	2	42
24	1	50
32	2	25
46	2	45
58	2	45
72	1	0

TABLE 25. CORN POLLEN STORED AT 11° C. UNDER RELATIVE HUMIDITIES OF 35 PER CENT AND 50 PER CENT. 1919

Length of storage	Ears pollinated		Fertilization	
	35 per cent humidity	50 per cent humidity	35 per cent humidity	50 per cent humidity
Hours	*Number*	*Number*	*Per cent*	*Per cent*
9	2	2	0	20
26	2	2	0	15
34	3	2	5	22
49	2	2	7	0
58	2	2	0	0
72	1	1	15	0
74	1	2	10	7
98	2			
100		2		0
109		1		0

humidity. Altho the results of corn-pollen storages are not conclusive, it is justifiable to say that fairly low temperatures (5°–10° C.) are more favorable than high temperatures or temperatures below freezing. Pollen lives longer at moderately high humidities (50–70 per cent) than in a dry atmosphere. However, if the humidity is too high, the pollen becomes sticky. Under the optimum conditions, as stated above, good, virile corn pollen should live for three days. The results show that pollen varies greatly in different seasons, however.

Possible causes of death of corn pollen

Loss of moisture

Andronescu (1915) found that corn pollen lost moisture rapidly when exposed in the open air or in a desiccator. He concluded that death was caused by this drying out. The following experiments were performed to gather additional data. Several grams of fresh corn pollen were spread out evenly on a large watch glass and carefully weighed. The watch glass was then placed in a desiccator and weighings were made as shown in tables 26 and 27. From a similar, but unweighed, sample, adjacent to it, pollinations were made at the same time that the weights were taken.

In a dry atmosphere, corn pollen loses moisture rapidly. Some of this loss in weight is obviously due to the carbon dioxide given off in respiration, but the calculated correction for this loss is only 6 per cent for the figures given in table 26, and 9 per cent for the values in table 27.

TABLE 26. POLLEN IN DESICCATOR OVER CALCIUM CHLORIDE AT 25° C.

Age	Ears pollinated	Fertilization	Water lost
Hours	*Number*	*Per cent*	*Per cent*
0	2	75	0
2	1	60	11
4	1	80	26
6	1	70	37
8	2	40 60	48
10	2	5 65	58
12	2	1 20	79
23	2	0–10	94

TABLE 27. CORN POLLEN IN DESSICATOR AT 25° C. AND 35 PER CENT HUMIDITY

Age	Ears pollinated	Fertilization	Water lost
Hours	*Number*	*Per cent*	*Per cent*
0	1	70	1
2	1	60	12
7	2	36–55	26
10	1	30	43
23	1	1	74

However, pollen remains viable after considerable desiccation. Thus, table 26 shows that fertilization took place even when 88 per cent of the water content had disappeared. In these experiments, the pollen was spread out on the watch glasses in as thin layers as possible, in an attempt to get the same amount of evaporation from each grain. It is probable that the few successful pollinations, after twelve and twenty-three hours, respectively, were due to pollen grains so favorably situated as to hold a larger amount of water. However, the results show that grains may lose from 40 to 50 per cent of their water without materially impairing their viability.

Experiments on respiration

In addition to desiccation, other factors which might impair viability suggested themselves. Since the moisture content of corn pollen is high, respiratory activity would probably be great. As a result, exhaustion of stored food might occur, and this would probably be accompanied by protoplasmic changes.

Respiration was first determined. Due to the small amounts of material available, difficulty was experienced in finding a method by which such small amounts of carbon dioxide could be accurately measured. Truog's (1915) method, as modified by Gurjar (1917), was finally used. This method consists essentially in catching carbon dioxide in a special form of absorption tower, containing standard strength of barium hydroxide, and titrating the remaining alkali against a standard acid. The results are given in table 28.

As was expected, the respiratory activity was high, diminishing rapidly in a dry atmosphere. However, it was not rapid enough to exhaust

TABLE 28. RESPIRATION OF FRESH CORN POLLEN AT A TEMPERATURE OF 25° C

Time	Weight of pollen	Carbon dioxide per gram per hour
Hours	*Grams*	*Milligrams*
2 5	6	2 11
3 0	6	1 71
3 0	6	0 36

all the stored carbohydrate within the several days that corn pollen normally retains its vitality.

Starch content of pollen

Microchemical tests show corn pollen to consist almost entirely of starch. In dead pollen, there is no apparent diminution in the starch content. Actual chemical analysis, using Sachsse's method, gave the results shown in table 29

TABLE 29. CARBOHYDRATE ANALYSIS OF CORN POLLEN

Age	Fresh substance	
	Starch	Reducing sugar
	Per cent	*Per cent*
Fresh	15 2	0 23
4 days ...	13 6	0 46

It is evident, therefore, that the stored food is not exhausted before death occurs.

Amylase activity

Since starch is the chief reserve carbohydrate, amylase must be an important enzyme. Determinations of amylase activity, with both fresh and dead pollen, were made by the following method. A weighed quantity of pollen (0.1 gram) was ground in a mortar with a few drops of distilled water until maceration was complete, after which it was filtered, and 2 cubic centimeters of the extract was added to 10 cubic centimeters

of 1-per-cent soluble starch. After twenty-four hours digestion at 30° C., the reducing sugar was determined. The results showed no decrease in amylase activity of pollen one week old below that of fresh pollen. The amylastic activity of seven-months-old corn pollen showed a marked diminution. This has no significance, however, as corn pollen remains viable for only a few days.

Catalase activity

Catalase activity was also determined. The method of extraction was similar to that for amylase. The Bunzell (1914) apparatus, graduated to read positive pressures, was used. Determinations were made at 25° C. The results (table 30) are the average of five determinations for each age of pollen.

TABLE 30. CATALASE ACTIVITY OF CORN POLLEN

Age of pollen	Reading after 1 minute	Reading after 2 minutes	Reading after 3 minutes	Reading after 4 minutes
Hours	*Millimeters*	*Millimeters*	*Millimeters*	*Millimeters*
6	4 3	7 1	8 7	9 8
38	3 6	5 7	6 9	7 6
58	2 8	5 3	6 2	6 9
106	2 8	5 3	6 2	7 0

As was expected, catalase activity seems to parallel respiratory activity, as was found by Appleman (1916) with the potato; but there is no indication that it has any relation to viability. Dead pollen still shows some catalase activity. Calculated in grams of fresh substance, the catalase activity is much lower than in Antirrhinum pollen.

From these experiments, the author must agree with Andronescu (1915) that the death of corn pollen is normally due to drying out, and not to exhaustion of stored food or to loss of enzymes. This is borne out by the results of the storage experiments, in which the high humidities prolonged life. Nevertheless, the pollen can resist desiccation to a considerable degree without impairing its viability. Even at high humidities, which lessened evaporation, the life of the pollen was not greatly prolonged. Some other factor, such as protein precipitation, may, therefore, be operating.

Resistance of pollen to extremes in temperature

The results obtained by various workers show that pollen is very resistant to low temperatures. It is much less sensitive than the stigma.

Goff (1901) found that plum and cherry pollen germinated after exposure to a temperature of −20° C.; raspberry pollen withstood a temperature of −23° C. Pollen of plum and cherry, confined for five days at a temperature of 20° C. in a saturated atmosphere, failed to germinate, while at 10° C. they germinated freely. Goff concluded from this that if the weather remained cool, a prolonged rainy spell would not be as injurious as at a higher temperature.

Ewert (1911) subjected apricot and peach pollen to a temperature of from −8° to −15° C. for a period of from two to three hours. The results were not uniform, altho high resistance was shown.

Sandsten (1910) found that freezing did not seriously injure apple, pear, and plum pollen, while less than 50 per cent each of the peach and apricot pollen were killed. A temperature of −1° C. caused permanent injury to the stigma of apple, pear, peach, plum, and cherry.

Chandler (1913) determined that apple pollen, when dried, would withstand a temperature as low as from −8° to −13° C. for eighteen hours. At −4° C. apple and cherry stigmas were killed, and of the peach stigmas, 43 per cent were killed at that temperature.

The low water content of Antirrhinum pollen suggests that it possesses considerable resisting power to low temperatures. The success attending the storage at freezing temperature, and even at a temperature of −30° C., led the author to try lower temperatures. Pollen was placed in stoppered test tubes and frozen in liquid air, with the results shown in table 31:

TABLE 31. RESISTANCE OF ANTIRRHINUM POLLEN TO TEMPERATURE OF LIQUID AIR

Time in liquid air (minutes)	5	15	15*	30
Germination (per cent)	60	60	60	60

* After being in an ice-salt mixture for 30 minutes

The germination was equally vigorous in all treatments, and even longer germ tubes were produced by pollen which had been frozen. The rate of the fall in temperature had no effect. No pollinations were made, but since germination was so vigorous the pollen undoubtedly was able

to effect fertilization. As the temperature of liquid air is somewhere near −180° C., the resistance shown is very remarkable.

Corn pollen is not able to withstand such low temperatures. Andronescu (1915) mentions the stimulative effect on corn-pollen germination of a temperature of from 8° to 14° C. In the storage experiments, there is a record of corn pollen which fertilized after forty five hours storage at 0° C. At −17° C., the pollen was dead after twenty-four hours. It is probable, therefore, that it cannot withstand a temperature much below freezing.

Antirrhinum pollen also is able to resist fairly high temperatures, as is shown by table 32. Other results, not included in the table, were similar.

TABLE 32. ANTIRRHINUM POLLEN STORED AT 52° C.

Time of storage	Germination	Length of germ tubes
Hours	*Per cent*	
11 75	75	Short
12 25	75	Short
12 75	50	Short
13 75	60	Short–medium
14 25	30	Short
14 75	10	Short
15 25	15	Short

Altho germination resulted after storage at this high temperature, it was weak and most of it abnormal in appearance, the germ tubes being short and swelled at the apexes. It is doubtful whether any fertilizations would have resulted from pollinations made with this pollen.

At the time when these experiments were made, the behavior of the pollen subjected to the high temperatures impressed certain facts on the mind of the author. Death seems to be progressive, with no point of absolute distinction between live and dead pollen. Germination became weaker and weaker as the duration of subjection to the higher temperature increased. This germination was abnormal but there was always the uncertainty as to whether the pollen was really alive. Living protoplasm is organized, while dead protoplasm is disorganized. Disorganization cannot occur quickly but must take place in stages, the rapidity being

dependent on the kind and intensity of the adverse condition. While these changes are going on, it is naturally difficult to judge whether or not the protoplasm is viable.

DISCUSSION OF RESULTS

The results of the studies with the pollen of *Antirrhinum majus* (snapdragon) and of *Zea Mays* (corn) show the striking dissimilarities between them. In the pollen of Antirrhinum, metabolic activity is weaker than in the corn pollen, as evidenced by less respiration, lower water content, and greater ability to withstand extremes in temperature. It would seem that the factors influencing longevity of Antirrhinum pollen are the same as in certain kinds of seeds. Desiccation, exhaustion of stored foods, and decrease of essential enzymes do not appear to be important. These same factors have not been found to be important in the loss of vitality of the seeds. Altho the author has no data to substantiate this, the theory of Crocker and Groves (1915) that death is caused by slow precipitation of proteins within the protoplasm, seems to be the most logical. The increase in reducing sugars, with increasing age, is evidence in favor of this theory, for it shows that some readjustment is taking place.

When corn pollen is subjected to normal atmospheric conditions, drying out undoubtedly determines the duration of vitality. When stored under conditions of high humidity, however, the vitality is not greatly prolonged. Altho respiratory activity is great, no marked loss of reserve materials occurs. As with Antirrhinum pollen, some destructive change must be going on within the protoplast. A change in the protoplasmic emulsion, such as precipitation, would affect the imbibitory powers of the colloids and might cause the excretion of water noted in the experiments.

With pollen, one must distinguish two degrees of vitality, one which can bring about germination and short tube growth, and another which will cause fertilization to take place. The author has given considerable evidence in these experiments that a pollen grain may germinate without ever functioning in fertilization. It is an open question whether this is due merely to the inability of the pollen tube to reach the ovary. Pollination experiments, under favorable temperatures, on short styles or styles of which the major parts have been severed, with a study of tube growth within the style, would shed some light on this.

The results from the storage experiments with pollen were exceedingly variable. Many factors that are difficult to control may influence the results. Pollen produced in different seasons and under diverse conditions is, in some way, physiologically different, as is shown by the differences in water content, the different optimum sugar concentrations required for germination, and the variations in the duration of life. Temperatures at pollination time, especially if unfavorable, may also influence results. It is an established horticultural fact that a larger "set" of fruit occurs on "selfed" varieties in seasons when the temperatures are most favorable for pollen tube growth. In the corn-storage experiments, where field experiments were made, it was, of course, impossible to control the temperature. In the Antirrhinum-pollen-storage experiments, all plants were grown in the greenhouse, so this factor was probably negligible.

The difference in resistance of the two kinds of pollen to extremes of temperature was striking, altho it was about what one would expect. Corn pollen with a high water content and high respiratory activity was more susceptible to injury than was Antirrhinum pollen with its low water content and weak respiratory activity. If death is due to an irreversible change of the protoplasmic system, a protoplasm like that of Antirrhinum pollen would be more resistant because of its low water content and, consequently, more stable, gel-like emulsion.

According to Harvey (1918), in addition to water content and metabolic activity, the basicity of the protoplasm also influences the resistance to low temperatures. In these studies, no hydrogen-ion determinations of pollen protoplasm were made.

SUMMARY

Pollen of snapdragon (*Antirrhinum majus* L.) germinates in any concentration of cane sugar up to 30 per cent. The most favorable concentration varies from 10 to 25 per cent, depending on the conditions under which the plant has been grown.

The most favorable temperature for the germination of Antirrhinum pollen is about 25° C.

The moisture content of Antirrhinum pollen varies from 10 to 20 per cent.

Cane sugar is the chief reserve carbohydrate in Antirrhinum pollen, the amount ranging from 8 to 10 per cent of the fresh substance.

Antirrhinum pollen remains viable longest under conditions of low temperature (0° to −17° C.). The longevity decreased when pollen was stored in oxygen or at reduced atmospheric pressures. There is some evidence that high percentages of carbon dioxide in the atmosphere favor longevity. The maximum duration of germinative ability was 670 days, and of fertilizing power 161 days.

The death of Antirrhinum pollen is not due to desiccation, exhaustion of stored food, or weakening of essential enzymes.

Antirrhinum pollen is extraordinarily resistant to extremes of temperature, being able to withstand one as low as −180° C. and one as high as +52° C.

Corn pollen is difficult to germinate. The optimum concentration for germination varied, depending on the conditions under which the plant had been grown. The best germination resulted in a 15-per-cent cane-sugar solution plus 0.7-per-cent agar.

The moisture content of corn pollen was between 50 and 60 per cent, depending on the conditions under which the plants had been grown.

The chief reserve carbohydrate in corn pollen is starch. Analyses showed that about 15 per cent, expressed in percentage of fresh substance, was present.

Corn pollen remained viable longest under conditions of moderately low temperature (5° to 10° C.) and moderately high humidities (50 to 80 per cent). This pollen was killed at a temperature of −17° C. The maximum duration of retention of fertilizing power was from seventy to eighty hours.

Under normal conditions, the death of corn pollen is caused by desiccation. However, since life is not greatly prolonged by storage under conditions which retard evaporation, moisture is not the only important factor.

Pollen may germinate in an artificial medium and yet be incapable of fertilizing a flower.

ACKNOWLEDGMENTS

The author acknowledges with pleasure his indebtedness to Professors Lewis Knudson and O. F. Curtis, both of the Laboratory of Plant Physiology at Cornell University, for much valuable advice and criticism rendered thruout this work, and to R. S. Nanz, of the same laboratory, for his aid in collecting data.

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Memoir 42, *Bean Anthracnose*, the tenth preceding number in this series of publications, was mailed on January 30, 1922.

Memoir 43, *Variations in Bacteria Counts from Milk as Affected by Media and Incubation Temperature*, was mailed on November 10, 1921.

Memoir 44, *Attachment of the Abdomen to the Thorax in Diptera* was mailed on December 30, 1921.

Memoir 45, *The Embryology of Tulipa*, was mailed on January 30, 1922.

MAY, 1922 MEMOIR 54

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

HORSE RAISING IN COLONIAL NEW ENGLAND

DEANE PHILLIPS

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

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HORSE RAISING IN COLONIAL NEW ENGLAND

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DEANE PHILLIPS

With the rapid rise of the sugar industry in the West Indies during the latter half of the seventeenth century, the continental British colonies in America were called upon to serve as the main source of supplies for the sugar plantations. An important trade grew up, especially with the New England region, in which the islands received lumber, fish, foodstuffs of various sorts, cattle, and horses. In return the northern colonies obtained sugar, molasses, rum, dyestuffs, and — of especial importance to New England — specie in various forms which could be used for purchasing manufactured articles and other needed supplies from England.

Horses were used on the sugar plantations to turn the rollers of the cane-crushing mills, to haul the cane from the fields, and to transport sugar and supplies. They were in demand for saddle purposes also. As far as New England was concerned, there is ample evidence that the exportation of horses to supply this need of the sugar islands formed a very important part of the commerce which was carried on between the two groups of British colonies in the New World, and that it was equally important in the trade which grew up between New England and the French West Indies when these islands also began the cultivation of sugar. The observations of contemporary writers, the reports of the various colonial governors to the Board of Trade in London, port records and various commercial statistics of the period which have been made available by modern research, and many other scattered sources of information, indicate that this was the case.

It is apparent that the development of such an export trade in horses must have stimulated a corresponding development of horse raising on a commercial scale. In this memoir an attempt has been made to gather together such widely scattered data as are available concerning this early agricultural enterprise of New England, and to trace its development and extent during the colonial period. Since, from its nature, this raising of horses was intimately bound up with the sugar

trade of the West Indies, it has seemed advisable to give some attention also to the growth and development of the latter industry.

SOURCE AND EARLY DEVELOPMENT OF NEW ENGLAND HORSES

It is not at all certain that to the early colonists New England appeared as stern and inhospitable a shore as we are sometimes led to believe. Hardships there were in plenty, and much real privation and want, but, on the other hand, the country gave to them bountifully in many ways of its own. Not the least of its advantages in the eyes of the first settlers was the comparative abundance of pasture and grasses suitable for hay, which assured an easy support for livestock in numbers sufficient for the colonists' needs.

This feature of the country is frequently mentioned in letters written to friends in England by the early settlers and in the accounts of travelers. Thus the Reverend Mr. Higginson (1),[1] writing in 1629, describes the abundance of grass "which groweth everywhere, both verie thicke, verie longe, and verie high in divers places"; and in regard to livestock he records further, "it do prosper and like well this countrie." Another writer (2), possibly too ardent in his admiration for the new land, compares the abundance of pasturage to "Hungaria." Josselyn (3), in his visits to New England, also seems to have been impressed with its possibilities along this line, and writes in 1675 of the "broad vallies supplied with ample forage as well as that to be found in clearings in the forests."

The native grasses which furnished this forage were mainly of two sorts—foul-meadow grass and herd-grass, or timothy (4). English grasses were introduced at an early date and were found to grow well in the new land (5). Both the native grasses made good hay, and this fact rendered it possible to keep livestock with little difficulty in spite of the rigors of the New England winters. The colonists were thus enabled to increase freely the number of their cattle and horses in proportion as they found them useful. As is shown later, they did not fail to avail themselves of this opportunity, and the increase that took place was a rapid one.

[1] Numbers in parentheses refer to the list of citations beginning on page 936. Sources cited are given in full in the list beginning on page 936.

USEFULNESS OF HORSES TO THE COLONISTS

Cattle and horses were of service to the colonists in many ways. The neat cattle furnished them food, hides for leather, and oxen for draft purposes. Sheep were valued chiefly for wool. Horses served to some extent for draft, but for ploughing and other heavy work they were found less serviceable than oxen. Their most important use was to furnish means of rapid transportation from place to place. In the earliest days of the settlements most of this travel was on foot or in small boats (6), but by 1652 a New England writer (7) could boast of the "wild and uncouth woods filled with frequented ways and rivers overlaid with bridges passable for both horse and foot." This indicates in a general way the transition that soon took place, so that horses became of steadily increasing importance as the settlement of the country proceeded and the towns became more numerous and widely separated.

In the difficulties with the Indians, horses were of especial advantage to the colonists. Not only was this true in the case of offensive operations against the savages, but in the frontier troubles which were always imminent the possession of horses enabled the settlers to bring aid quickly to one another when attacked and thus saved many an isolated settlement from extinction. That the colonists realized this advantage is apparent from the pains which they took to prevent any horses from coming into the hands of the natives. In Plymouth (8), in Massachusetts Bay (9), and in Connecticut (10), laws were passed to prevent the selling of any horses to the natives, and even as late as 1665 it was only after considerable debate that the Plymouth court allowed one such sale to be made to a friendly Indian for purposes of "husbandry" (11).

Lastly, it is interesting to note that horse racing was not unknown even in the early days of the Puritan settlement in the Massachusetts Bay colony, where the court vents its dire condemnation on "certain euill and disordered persons" who engaged in such a breach of public decorum (12). At a later date, however, such racing came to be a recognized sport in Boston (13), and especially in Rhode Island, where races were very common and often for high stakes (14). These practices were not frequent in the early days, however, and came to be

tolerated only after the country was well settled and customs had changed considerably.

EARLY IMPORTATIONS

The first colonists who settled at Plymouth in 1620 brought neither horses nor cattle with them to the new land, and it was not until four years later that the first neat was brought over (15). In the same year the correspondence of Governor Bradford indicates that "a bull and 3 or 4 jades" were to be shipped to him from London to be sold in the colony (16). The first record of the actual presence of a horse in Plymouth seems to be in 1632. Governor John Winthrop, of the Massachusetts Bay colony, describes in his diary a journey made to Plymouth in that year, partly by boat and partly on foot, and states that on his return he was sent a part of the way on "the Governor's mare" as a mark of special respect (17).

However, from some source — probably England, but possibly Holland, with whose ships the colonists had traded (18) — the Plymouth settlers had by 1632 obtained a considerable supply of cattle, for it is stated by Governor Bradford that by this date many persons had been enriched by selling corn and cattle at high prices to newcomers in both Plymouth and Massachusetts Bay and had "spread out on farmes" for the purpose of raising more (19). As to the number of horses in Plymouth at that time, however, no information can be gleaned from Bradford's narrative, for he, in common with other writers of the period, uses the term *cattle* more or less indiscriminately to cover any sort of livestock, including horses.

The richer Massachusetts Bay colony seems to have been better supplied than the colony at Plymouth. The fleet that arrived with its numerous settlers in the year 1629 brought over also a considerable number of horses and cattle, one hundred and fifteen head in all (20), among which were thirteen horses (21). In the following year two ships that brought over Governor Winthrop and the second group of colonists had on board two hundred and forty cows and about sixty horses, as is learned from Winthrop's letters (22). Some of these animals died while *en route* and it is not certain just how many were added to the stock of the colony, but among the horses that survived there were both mares and stallions (23).

After the arrival of these early settlers, the succeeding decade saw the landing of a steady stream of new colonists about the bay. It is reasonable to suppose that they also brought many horses, but specific references to such importations are not frequent. Sir Ferdinand Gorges in 1632 wrote from England to Captain John Mason in Massachusetts promising to send over several at the first opportunity (24), but no mention is made of their arrival. Winthrop also records a few importations, but in a casual and incidental fashion which implies that his register makes no attempt at completeness in this respect. Of those noted by Winthrop, the first is in 1633, when he mentions the arrival of the ship *Bird* with four mares on board (25), and in the same year the *Bonaventure* with two, four having been lost in transit (26). In 1635 Winthrop speaks also of the arrival of a Dutch vessel with "27 Flanders mares ..... and 3 horses" (27). This last-named ship had cleared at the Texel five weeks previously, and had thus made an unusually quick voyage and one notable for the fact that none of her cargo of livestock had been lost *en route*.

During these early years, also, both Winthrop and Bradford record in their journals the frequent arrival in the bay of ships having cattle on board, and it is probable, for reasons already given, that these "cattle" often included some horses. The number of such arrivals was certainly large. Winthrop, for example, notes that in 1634, "during the week the court was in session there came in six ships with store of passengers and cattle" (28). In the same year there were fourteen ships in one month which cast anchor either in Salem or in Boston (29). Many more arrivals probably went entirely unrecorded, and therefore the scantiness of the record does not necessarily mean that horses were not being brought into the country in considerable quantities. That they were being imported in large numbers is, in fact, the only possible conclusion to be drawn in view of their great abundance a few years later — to confirm which there is plenty of evidence, as will be shown presently.

SOURCES OF NEW ENGLAND HORSES

Since the early importations undoubtedly furnished the basic stock from which two noted American breeds — the Narragansett pacers and the still more famous Morgans — were later developed, it is worth while

to consider briefly the sources and the general characteristics of these first imported horses.

In view of the lack of any direct evidence to the contrary, it is fair to assume that the first shipments were mainly from England and of the small nondescript type which at that time made up the bulk of the English horses (30). There was, however, some admixture of other blood. In the primary importation into the Massachusetts Bay colony in 1629, three at least are mentioned specifically as "having come out of Leicestershire" (31), which at that time was the source of a more or less distinct type of horse of a sort better than the average (32). The importation of Flemish mares also has been noted. Wallace contends that these latter were not Flemish but were rather of a Dutch type (33), but his conclusion is based merely on the fact that the vessel cleared from a Dutch port — which does not seem a very valid reason for controverting Winthrop's specific statement as to their Flemish origin, especially since Flemish horses were well known at that period as a distinct type.

There is one other possible source of some of the New England horses which deserves consideration, especially because it may tend to explain in some measure the persistently small size of these horses, even when carefully bred — as later they were in Rhode Island and Connecticut — and, further, the constant occurrence among them of individuals possessed of a natural pacing gait. This possible progenitor is to be found in the Irish hobbies, a race of small, hardy, wild ponies existing in Ireland during the first part of the seventeenth century. These horses were in great demand in England for saddle purposes, and were exported thence in such quantities that they are said to have become practically extinct in Ireland before the year 1634 (34). They were well known in England, and their natural pacing gait made them especially desirable in any place where travel was of necessity on horseback (35); it is not at all improbable, therefore, that some of these found their way to New England, where they would have been especially serviceable. There seems to be no direct evidence to this effect, but any comparison of such fragmentary descriptions of the two as are available discloses a rather striking similarity between these Irish hobbies and

the famous Narragansett pacers which were later developed in Rhode Island.[2]

FREE RANGE AND ITS EFFECTS

From the very earliest period of New England history it was customary to allow both horses and cattle to run at large on the public commons. At times some provision for a herdsman was made, but as the herds increased in numbers and the settlements became more scattered the animals began to roam more or less at will about the settled areas and often strayed away for considerable distances into the forest or were lost completely. Winthrop records a happening of this sort in a letter written to Governor Endicott on behalf of a widow whose horse had been impressed for military service. Pleading her need for the one that had been taken from her, he says, "She hath another horse but has not seen him for several months" (36). Strays of this sort were numerous and this often led to many difficulties of ownership, which in time compelled definite legislative provisions to be made.

Where horse raising developed, as it did later, on the islands of Long Island Sound and on the water-guarded points and necks of Rhode Island, this free range was not a serious problem. But where the horses and cattle were running loose about the towns in a semi-wild state and in ever-increasing numbers, many difficulties were bound to arise. The chief trouble came from damage done to gardens and crops by herds of these equine and bovine marauders. At first "all greate cattle" were herded by day by a public herdsman, and the owners were held responsible for any harm inflicted by their animals after nightfall (37). But soon the burden was put on the other side, and in Massachusetts Bay, for example, in 1642 the court repealed the former act and provided that "every man must now secure his own corn and meadow against damage" (38). It was provided further that only in case animals running at large had broken through an admittedly strong fence could the person suffering the damage have any redress. Complaints for damages of this sort appear continually in the court records of all the colonies, and it was apparently a cause of endless litigation, which persisted until a late date.

[2] A more detailed discussion of the origin of the Narragansett pacers is given on page

Another difficulty met with as a result of open-range conditions was that of deterioration of the breed. Whatever may have been the source of the New England horses, it is clear that the promiscuous breeding of the semi-wild animals on the commons could not be conducive to the perpetuation of their best characteristics, although it may have resulted in a certain hardiness by weeding out the ones unable to stand the rigors of this wild life. At any rate, efforts were made before long to prevent the breeding of the obviously unfit. In 1668 the court in Massachusetts Bay declared: "Whereas, the breed of horses is utterly spoyled whereby that useful creature will become a burden..... be it enacted that no stone horse above two years old be allowed on the commons or at liberty unless he be of comely proportions and fourteen hands in stature" (39). The owner of a horse found in violation of this statute was to be fined, and later the amount of the fine was raised. Plymouth (40) and Connecticut (41) passed similar limitations, the minimum stature in the latter case being set at thirteen hands. These restrictions seem to have been fairly well enforced but could obviously result in little improvement of the breed as long as complete open-range conditions prevailed.

One of the perplexities in all these cases of damages, after horses and cattle had become numerous, was for the person whose premises had been invaded to recognize whose animal it was that had done the damage. The same difficulty was met with in fixing the fines for undersized stallions found running at large. Often these horses and cattle were even strays from a neighboring town, which made the problem still more complicated. This led to the passage of acts compelling the branding of all animals with both the mark of the private owner and that of the town of his residence. The general court in Massachusetts Bay passed such an act in 1647, and in its records are enumerated the marks of thirty-three different towns under its jurisdiction at the time (42). In 1656 the New Haven colony compelled horses to be branded (43), and the other Connecticut towns did the same in 1665 (44). Rhode Island had a similar provision (45). In the latter plantation in 1680 thirty wild and unmarked horses were ordered caught and sold and the proceeds employed to build a prison and stocks (46). This was the usual fate of unbranded animals or persistent strays. In 1661 the court at Plymouth, "on complaint of some that certain horse-

kind belonging to Rhode Island are found goeing within our libertys.... to the great annoyance of Indians and English," ordered that such animals should be treated as common strays and sold (47).

INCREASE IN NUMBER OF HORSES

In the two or three decades following the first importations there was a rapid increase in the number of horses in New England, and they became abundant not only in the region about Massachusetts Bay but also in the newer settlements in Connecticut and Rhode Island. As the colonists pushed into these latter areas they took horses and cattle with them from the earlier settlements, and, finding the new regions in some places especially suitable for the raising of livestock, they began to engage in it on a considerable scale, so that by 1650 or soon afterward there had come about an abundance of both horses and cattle through the whole New England territory.

The increase which thus took place is brought out clearly by the course of prices during the period. In the years of the great immigration that followed the first settlements on Massachusetts Bay, these prices were rather high. Winthrop, in 1633, rates mares as being worth £35, and cows from £20 to £26 (48). Two years later the Flanders mares, the importation of which has already been noted, sold for £34, and heifers brought in by the same ship sold for £12 each (49). During the next few years the great number of settlers arriving caused prices to rise even higher, and, as Bradford records, "ye anciente planters which had any stock begane to grow in their estats and spread out on farmes to raise more" (50).

By 1640, however, the supply had apparently overtaken the demand and prices began to fall (51). By 1645 this decrease had gone so far that Winthrop speaks of a horse the price of which he gives as £10 as a "costlie horse" (52). In 1653, however, horses were still rated by the Massachusetts Bay court at £16 (53), but thirteen years later, in Connecticut, they had fallen to half that amount (54), and in 1668 the Massachusetts Bay court reduced the rate from £10 to £5 (55). Finally, in 1677, the rate was still further reduced in Massachusetts Bay, and horses were ordered to be received at a rate of £3 for each horse or mare above three years old and 40 shillings for two-year-olds (56). In

the last-named case the court stated specifically as its reason for the reduction that horses had for some time been worth much less than the amount previously fixed by law. During this period of falling prices, the number of persons in the country had steadily increased, roads were being established, and new agricultural lands had been opened up — all of which would result in an increased demand for horses. It appears, therefore, that the increase in their numbers must have more than kept pace with the development of the country, and that the decrease in prices was due to the abundance of the supply rather than to any decreased need for their services.

There is much other evidence to indicate that by the middle of the seventeenth century horses had become very abundant. In 1647 those running wild in Massachusetts Bay were so numerous and were doing so much damage as to call for legislative interference (57), while Maverick, writing a little more than ten years later, says, "it is a wonder to see the great herds of cattle ..... and the great number of horses besides the many sent to Barbadoes and the other Carribee islands" (58). The same condition is attested by John Winthrop the younger, writing from Connecticut in 1660 (59), and by the report of the Commissioners to New England presented to the Board of Trade in London in 1665 (60). By 1675, according to William Harris, who had been sent out by the Board of Trade, the country had so many horses "that men know not what to do with them" (61).

A still further indication of the plentiful supply of horses in New England is the fact that by this time these colonies had begun as a source of supply for other colonies. In 1642 Massachusetts Bay was being called upon to furnish a shipment of horses to Lord Baltimore's colony in Maryland (62), and in the report to the Board of Trade in 1665, already mentioned, horses are named as one of the exports of Massachusetts to Barbados and Virginia. A letter written in 1656 by Secretary von Tienhoven, of the Dutch West India Company, indicates that at that date horses were being obtained from New England by the Dutch on the Hudson River (63). The letter in question advises prospective settlers in the New Netherlands to take no horses with them to the new land, because "they can be got at reasonable expense from the English who have plenty of them." There is appended to a

table of prices in "New England" for horses, cows, and hogs; so there can be no doubt as to which of the English settlements Von Tienhoven had in mind.

It is thus apparent that by about the middle of the century or a little later, New England had come to have an abundance of horses more than sufficient for its own needs. Natural increase under free-range conditions would account for such large numbers only if it were assumed that the importations during the early years of settlement were far more numerous than have been recorded, or else that such importations continued throughout the whole period — which does not seem very probable. During the latter part of the years described, however, the exportation of horses, which was just beginning, had as a result the stimulation of horse breeding for this purpose in a more careful manner, and probably accelerated to some extent the rate of increase.

With the development of this export trade begins the second phase of horse raising in New England, resulting in many changes throughout the area and in the establishment of horse breeding as an important and extensive industry in certain favorably located sections.

THE BEGINNING OF THE EXPORT TRADE IN HORSES

As has already been indicated, some horses were exported from New England to the other continental colonies at an early date. Such shipments, however, never came to be of any great importance, and are worthy of mention chiefly to show the relative abundance of horses in New England as compared with their numbers in the neighboring colonies. The main demand that resulted in the exportation of New England horses came from the sugar plantations in the West Indies, where both horses and cattle were needed for draft purposes, to haul the cane from the fields, to transport sugar and supplies, and to turn the heavy cylinders in the cane-crushing mills.[1] Horses were used for

[1] Oldmixon (*The British Empire in America*, vol. 2, p. 147) gives the following description of the operation of these cane-crushing mills: "They grind the canes thus in the mills: The Horses and Cattle being put to the tackle, go about, and turn by the middle Roller; which being cogged to turn others at the upper end, turn out. They all three turn upon the same centers which are of Brass and Steel, easily of themselves, that a Man, taking hold of one of the Sweeps with his hand, may turn all the rollers about; but when the canes are put between the rollers 'tis a cool Draught for five Oxen or Horses."

saddle purposes also by the sugar planters, who were willing to pay high prices for superior animals of this type.

That the New England colonies, rather than any of the other continental settlements, should have become the accepted source of supply for this demand from the sugar islands, resulted chiefly from the fact that they were the only ones which possessed a surplus of horses at the time when the demand first began to make itself felt, about the middle of the seventeenth century. In most of the other colonies there was an actual scarcity of horses, as in Virginia (64). The Dutch in New Netherlands, it is true, did actually export some horses during the year 1650, but an act was soon passed which forbade such shipments (65). It thus came about that in the early days of the sugar industry in the West Indies, New England had no real competitor among the continental colonies in supplying the growing demand for horses for the sugar plantations. Virginia furnished many cattle (66), and after 1700 the colony on the Hudson River, by that time in English hands, again began the shipment of horses; but New England's leadership in the trade was never seriously threatened during the colonial period.

The continental American colonies proved to be a convenient source of supply to the sugar islands of the West Indies, not only for horses and cattle but for many other commodities as well. The trade in horses, in short, was an integral part of the much more extensive commerce which grew up between the West Indies and the northern British colonies whereby the islands were supplied with timber, boards, staves, fish, and provisions of all sorts, in return for sugar, molasses, rum, dyestuffs, and, most desirable of all, Spanish dollars and bills of exchange on London. The extent of the export trade in horses at any particular period, therefore, was influenced by the condition of this commerce as a whole and by the changes that took place in the sugar industry itself. Wars, acts of Parliament, competition between the Islands — in short, all factors that aided, hindered, or changed the direction of this larger trade — had their effect on the exportation of horses. Certain changes in the manufacture of sugar which took place during the first part of the eighteenth century also tended to decrease the demand for horses. Since, therefore, the horse raising that developed in New England during the later part of the colonial period was essentially dependent on

this export trade, it is necessary in any further treatment of the subject to consider in some detail the rise and development of the sugar industry itself.

RISE OF THE SUGAR INDUSTRY IN THE BRITISH WEST INDIES

At the beginning of the seventeenth century, Europe was being supplied with sugar mainly by the Portuguese, from Madeira and, more especially, from their settlements on the mainland of South America, in Brazil. The English also had probably produced some sugar in South America, from Surinam, before ceding that colony to the Dutch by the treaty of Breda (67), but it was not until they had established a settlement in Barbados, one of the Windward Islands, that they began to be serious competitors of the Portuguese.

The colony in Barbados had been settled for some time before 1630, but for a considerable period it had produced only indigo, ginger, cotton, and "bad tobacco," which brought in but moderate returns. Sugar culture was introduced in or about the year 1642, and by 1650 the planters had grown proficient in its production and were shipping it to England in considerable quantities (68). The new industry met with remarkable success and within a few years the island had become very prosperous; lands had increased greatly in value, and the planters had amassed great wealth and were found living on a scale of surprising pomp and luxury. In 1661 King Charles II created thirteen baronets from among these planters, none of whom are said to have had an annual income of less than £1000 and some of whom had more than £10,000 a year. In the same year the trade of the island is estimated to have supported more than four hundred ships and the value of the exports is placed as high as £300,000 (69).

The great success of Barbados stimulated the growing of sugar on the other islands of the British West Indies. St. Christopher (which the English shared with the French), Nevis, Montserrat, Antigua, and lastly, after its capture from the Spanish in 1655, Jamaica, all came into the market with sugars and the trade grew at a rapid rate. The Navigation Acts, confining this commerce to British bottoms, soon made London the chief sugar mart of the world, whence the product was re-exported by British merchants. English sugars undersold those of

the Portuguese, and by 1670 the latter had been forced out of practically all the markets north of Cape Finisterre (70).

EARLY EXPORTATION OF NEW ENGLAND HORSES

The rapid development of the British sugar islands called for great quantities of supplies to carry on the work of the plantations, and, since the islands had few resources of their own, importations were necessary. Provisions from Ireland, slaves from Africa, shoes and other manufactured goods from Europe, as well as the products of the continental British colonies — the nature of which has already been indicated — all were brought into the islands, and of these supplies horses were a not unimportant item.

In the earliest days of the sugar industry, trade was still free and the Dutch and the Portuguese seem to have furnished the British islands with as many horses as were needed (71). With the stoppage of this trade by law and the increasing development of the plantations, however, recourse was had to England and to New England to supply the demand. During the period between 1649 and 1658 the importations of English horses were especially numerous. In those years there are recorded in the British Colonial Papers forty-eight different permits for such shipments, for a total of more than nineteen hundred horses (72). England continued to send horses until as late as 1667 (73), but the levying in 1654 of an export duty of 20 shillings a head (74) cut down the numbers considerably and hastened the shift in the trade by which New England at length became almost the sole source of supply for the islands. In that region there was no export duty except in Massachusetts Bay, where it was only sixpence, and the cost of transportation was much less because of the shorter distance, which resulted also in much smaller losses in transit.

The trade of Massachusetts Bay with the West Indies had already been established before the production of sugar in the British islands had come to be of importance, and so it is only natural that with the rise of the latter industry and the demand for horses the growing surplus of New England animals should receive the advantage of the outlet thus opened. As a result, horses were being shipped from Massachusetts ports fully as early as from those of England, for

the reasons given, the numbers exported soon exceeded those from the English ports. Concerning the beginning of this trade Winthrop writes in 1647: "It pleased the Lord to open to us a trade with Barbados and the other islands . . . which as it proved gainful, so the commodities which we had in exchange for our cattle and provisions, as sugar, cotton, tobacco, and indico were a good help to discharge our engagements with England" (75).

As to whether there were any horses among these "cattle" which Winthrop states were being sent to the West Indies, there is no evidence. The record of such exports is, in fact, much like that of the early imports into the country, and specific mention of such shipments is not frequent, even though more general statements, such as those to be found in the reports to the Board of Trade in London, indicate that they were taking place. In 1648 Winthrop notes in his journal the presence of a ship "lying before Charlestown with eighty horses on board bound for Barbadoes" (76), and this is probably the first recorded exportation of horses from New England to the West Indies. Wallace states (77) that there was a shipment of eighty head in 1640, but he does not give the source of his information and it is more than probable that it is this exportation of 1648 to which he refers, inasmuch as the demand for horses had hardly begun in Barbados as early as 1640.

The exportation of horses from New England in 1648 or before was evidently not limited to this one cargo, however, for a writer who styles himself Beauchamp Plantagenet, describing a visit to Barbados in that year, states that "New England sendeth horses and Virginia oxen" to turn the sugar mills in the island (78). In 1649 the Massachusetts Bay court passed an act forbidding the exportation of mares and placing a tax of sixpence on every gelding sent out of the country (79). This was obviously an effort in the main to protect the breeding stock of the area, and Massachusetts Bay urged that similar prohibitions be adopted by all the United Colonies of New England. The colony at New Haven was the only one to act on the recommendation (80), and in Plymouth and Rhode Island there continued to be no restriction on such shipments. That such a law was found desirable in Massachusetts Bay was due partly to military considerations, but the fact serves also as

an interesting side light on the extent of the demand for horses, for it is clear that at that time there was no great scarcity of them in the region.

The trade between Massachusetts Bay and Barbados was more or less interrupted during the period of the Commonwealth in England, as a result of the refusal of Barbados to submit to the new authority; but, in general, the exportation of horses from the colony continued on a considerable scale, and there is much evidence of the growing dependence of the islands on the New England region as a source of supply. The report of the Commissioners for New England to the Board of Trade in London in 1665 states that Massachusetts exported fish, pork, beef, horses, and corn to Virginia and Barbados (81). Inasmuch as horses are not mentioned as a product of any of the other colonies, in the report, it may be inferred that the region about Massachusetts Bay was still the chief source of supply among the continental colonies. In 1673 Captain Gorges was instructed by the Assembly of Barbados to insist to the English Parliament on the dependence of the island on New England for "boards, timber, pipe staves, and horses," to the end that no acts might be passed which would interfere with the trade (82). And in 1675 a certain "Mr. Harris of New England" gave an account of the trade of the country, in which he says that "to Barbadoes in exchange for horses, beef, pork, butter, cheese, flour, peas, biscuit, we have sugar and indigo" (83).

In 1700 Massachusetts Bay was still sending large numbers of horses to Barbados, and also to the Leeward Islands and to Jamaica. Toward the end of the century, however, many of the horses shipped were animals that had been raised farther inland and had been driven considerable distances to be sent out from the ports on Massachusetts Bay (84). This is shown, for example, by the correspondence of Wait Winthrop with his brother Fitz-John, of Connecticut, by which it appears that the latter was sending horses overland to Boston from his plantation on Fisher's Island, in Long Island Sound (85). There was thus taking place a shift in the raising of horses in New England, by which other regions than that about Massachusetts Bay were coming to be of increasing importance, especially as regarded the export trade.

As the settlement of New England proceeded, it was very soon dis-

covered that there were certain areas in Rhode Island and in Connecticut which were much better adapted to the raising of livestock of all kinds than the region first settled (86). These more favored areas were found mainly in the upper valley of the Connecticut River, along the shore of Long Island Sound, and about Narragansett Bay in Rhode Island. Here plenty of level, well-watered pasture lands were found, swamp grasses which made good hay were abundant, and in many places the grazing areas were intersected with salt-water ponds and lagoons which served to separate pasture land from cornfields far more effectively than any fence could have done. The damages and endless difficulties resulting from free range in other less favored sections made this last-named feature one of no mean advantage in the raising of livestock and in the improvement of the breed. The few cattle, sheep, and horses which the first settlers in these regions brought with them were soon augmented by others, and before long the obvious agricultural advantages of the new areas were being used to their full extent.

With the coming of the demand for shipment to the West Indies, horses and cattle were soon being raised for export in these more favored districts. Some horses were apparently being shipped from Newport as early as 1656, but there is some question as to whether this particular shipment did not consist of horses stolen from Massachusetts instead of animals raised on Narragansett Bay (87). In 1677, however, Captain John Hull wrote to one of his partners in the Pettiquamscut Purchase in Rhode Island, proposing to build a stone wall across Point Judith Neck, "so that no mongrel breed might come among them," and to raise a breed of "large and fair horses and mares" for shipment to the West Indies (88). This plan appears to have been put in operation, for not long afterward Hull wrote to a resident of the district, a certain William Hefferman, accusing him of stealing horses and further tartly offering to give him some horses that he might have no further need to indulge in such practices (89). By 1680 horses were being shipped from Rhode Island in sufficient quantities to be mentioned by Governor Sanford in his reply to the inquiries sent out by the Lords of Trade and Plantations, in which he states that "the princi-

pal matters which are exported among us is horses and provisions" (90).

In Connecticut, also, horses soon came to be a recognized commodity of trade. From the towns on the upper Connecticut River, as late as 1680 many horses were being driven overland to Boston to be sold, presumably for the export trade (91). The coast region of Connecticut had before this time begun a direct trade with the West Indies. In 1667 it is recorded that a vessel had been sent out from New London bound for the island of Nevis, from which twenty-six horses were lost overboard in a storm (92). Such other evidence as is available indicates that this was not an isolated shipment from New London. This port was, in fact, so situated as to draw not only on a fairly well-adapted livestock area in Connecticut, but also on the most important part of the Rhode Island area, and with the development that continued to take place it in time became the chief center for the exportation of horses from New England. In the period before 1700, however, New London had but made a beginning in this trade, and this was also the condition of Newport, Providence, and the river towns of Connecticut.

HORSE STEALING

One further development took place during the period just described, which casts an interesting side light on the extent of the export trade in horses and its effect on the New England region. This was the growing prevalence of horse stealing throughout all the colonies. One of the objects of the branding of horses and cattle, already described, was to prevent this practice. The brander in most of the towns was a dignitary of no small importance, and as a rule was required not only to brand each animal but also to keep a record of the operation in an official book together with a description of all the natural and artificial marks on the animal and the name and residence of the owner. In Rhode Island (93) and in Connecticut (94) there were fixed severe penalties for any person who took or attempted to take out of the town any horses or cattle without first informing the official brander and receiving his permission.

Branding alone, however, did not provide a very effective check on the stealing of horses and cattle. As the exportations grew in volume and more and more ports were engaged in the trade, it became increas-

ingly easy to conceal such thefts and the practice became surprisingly prevalent. Miss Caulkins, in her *History of New London* (95), has described as follows the conditions during this period:

> As the West India trade increased from year to year the raising of horses became very profitable and many farmers entered into it largely. Lands being unenclosed it was easy to run such horses off to a port where the mark of the owner was not known, or the mark itself could be altered. A bold rover in the woods might entrap half a dozen horses with ease and, shooting them off through Indian paths by night, reach some port in a neighboring colony; and before the owner could get track of them they were far off upon the ocean, out of reach of proof. Many persons otherwise respectable entered into this practice or connived at it. Men who would scorn to pocket sixpence that belonged to another seemed to think it no crime to throw a noose over the head of a horse running loose and to nullify the signet of the owner or engraft on it the mark that designated their own property.

Professional buyers, called "horse coursers" in the parlance of the time, went about the country gathering up horses into pounds for sale or driving them to ports whence they were shipped, and very few of these persons escaped the suspicion of having at one time or another enlarged a drove by gathering into it some to which they had no legal claim. Persons of considerable prominence also were implicated, as Miss Caulkins indicates; William Coddington, at one time governor of Rhode Island, seems to have been one of these (96).

Such delinquency increased greatly in the latter half of the century and the disclosures become more and more frequent. In 1668, as a preventive measure, the Massachusetts Bay general court ordered a toll book to be kept in every town, in which was to be entered a description of each horse, and a voucher was to be given to the owner to prove his property (97). It was necessary to present this voucher in case of any subsequent sale. As has been noted, both Rhode Island and Connecticut had passed laws forbidding the taking of horses beyond their jurisdiction unless first recorded by the town recorder. In 1684 court was held at Stonington for the trial of horse coursers. Two persons were convicted and sentenced to pay fines of £10 and to receive fifteen lashes (98). The court calls the offense "a crying evil" against which all well-disposed persons were bound to give aid. In 1700 a special court was held at New London for the sole purpose of trying horse thieves, and the penalties for such thieving were made more severe (99). Finally, in 1701 a toll book was ordered to be kept in

every seaport town in Massachusetts, in which were to be entered the number, description, destination, and vessel on which it was shipped; of every horse sent out of the colony, as well as the name of the owner of the horse and his place of residence. For any violations a fine of £10 was to be inflicted for each horse sent out (100).

The incentive for most of this stealing was, of course, the export trade to the West Indies, which made the thieving both possible and profitable. The prevalence and widespread extent of this practice is but one more indication of the importance and magnitude of the export trade itself during this period. It is therefore probably no exaggeration to say that by the year 1700, horses were being raised for shipment to the West Indies throughout the whole New England area — to such an extent had the trade developed in the space of fifty years. It is apparent, however, that by this time a shift was taking place in the center of the trade, from its early location in the ports of Massachusetts Bay to those of Rhode Island and, especially, Connecticut.

These shipments of horses were carried on the decks of the vessels engaged in the West Indies trade, so that nearly every ship could transport a few animals on the southward voyage. Since the ships engaged in the trade were numerous and since they usually made two trips a year (101), the possible shipments of horses were large. By the end of the period, also, a beginning had been made in the building of vessels with more ample deck space to provide room for the livestock shipments, and these "horse jockeys," as such vessels were called (102), played an important part in the West Indies trade during the century that followed.

INCREASING DEMAND FOR NEW ENGLAND HORSES FROM 1700 TO 1775

The exportation of horses, which by 1700 had become a well established part of the trade of New England with the British sugar colonies, continued on an increasing scale during the century that followed. About 1700, however, the demand for supplies for the islands began to be greatly augmented by the entrance into the market of the Dutch and French West Indies, which were beginning in their turn to develop the raising of sugar on an extensive scale. A steady increase in New England exports was a reflection of these changes that were taking

place in the sugar industry, and horses continued to be an important item in the exchanges. In the various ups and downs of the sugar trade, therefore, is to be found the explanation for corresponding changes in the raising of horses which took place in New England during the first half of the eighteenth century.

GROWTH OF THE SUGAR TRADE AND EXPANSION OF THE MARKET FOR HORSES

In 1698 a decree of the Royal Council of France allowed sugar from the French islands, which were at that time producing only small quantities, to be sent directly to any port in Europe. This proved a great stimulus to the development of the French colonies, and after the Peace of Utrecht the growth of these was rapid (103). Martinique, Guadeloupe, Dominica, and Santo Domingo — the French colony on the island of Hispaniola, or Haiti — all came into the market with sugars. Prices fell off sharply as a result of the increased production (104), and the British islands — partly, at least, because of the law compelling them to send their sugar first to England, from whence it was re-exported[1] — found it difficult to compete with the French, who were soon in a fair way to oust the British from their leadership in the trade (105).

The continental British colonies were not slow in taking advantage of the new outlet for their products which was thus opened up, especially as the trade with the French proved to be very profitable. The French home market was closed to the importation of rum — which, distilled from molasses, was an important by-product of the manufacture of sugar — and as a result the French planters were willing to sell their molasses much more cheaply than were the British. This molasses was eagerly taken by the New England traders in exchange for the usual plantation supplies, and was brought back to New England, distilled into rum, and used to advantage in exchanging for furs and in the African slave trade.

Most of the trade with the French islands was carried on by direct voyages to their ports, and some supplies were furnished in this way

[1] According to Ashley (*The British Colonies in America*, vol. 1, app. 1, p. 75) the exports from England during the period under discussion were as follows: 1713–1714, 10,000 hogsheads a year; 1715–1719, 17,000 hogsheads a year; 1733–1736, 2300 hogsheads a year; 1737–1739, not more than 450 hogsheads a year

to the Dutch, who were increasing their sugar production in Surinam. There grew up in addition a very considerable indirect trade by way of the barren Dutch island of Curaçao, where the Dutch had established a free port. This port soon became a great entrepôt for all the West Indies. Here were landed the supplies brought by the New England vessels, which returned home laden with sugar, molasses, and the other products of the islands, while the lumber, horses, provisions, and other supplies brought by them were either transferred directly to island vessels or put ashore and peddled out among the islands by the Dutch at their leisure (106).

During this time New England horses continued to be sent, as formerly, to the British islands along with the other customary supplies, but there is much evidence that they were equally important in the trade with the Dutch and the French. At Curaçao they were received in considerable quantities and many were put ashore on the neighboring islands of Boneiray (or Bonaire) and Aruba (107). Here they were kept until there was a call for them in the trade carried on at Curaçao. At Surinam no vessel was allowed to trade unless it brought in horses as part of its cargo (108), and the various reports to the Lords of Trade made by the governors of the continental British colonies indicate that this Dutch colony was a frequent destination for the horses sent out from their ports (109). Another and more confidential report made to the Lords of Trade in 1721 "On the State of the British Plantations in America" states that "the trade of Massachusetts Bay consists chiefly in the export of horses to Surinam and to Martinico and other French islands, which is a great discouragement to the planters in the British islands for without these horses French and Dutch could not carry on their sugar trade" (110). In 1743, Ashley, writing on the condition of the British colonies, also notes horses as one of the important items with which the French and the Dutch are supplied by the continental colonies (111), and his statement is confirmed by that of other contemporary writers and especially, by reports of the various British governors to the Board of Trade in London.

There are many other indications that this trade in horses between New England and the Dutch and French islands was extensive. Gov-

ernor Robert Lowther, of Barbados, writing to the Board of Trade as early as 1715, states: "It would be of great advantage to this place and to all his Majesty's Sugar Colonies, if there was made a law in England to Restrain His Subjects in North America from exporting Horses into any country not under his Majesty's Dominion, for the French at Martinique and Guadelupe and the Dutch at Soronam begin to rival us in the sugar trade and this is owing to the great Supplies of Horses they receive from New England" (112). Other British governors and numerous sugar planters continued to write to the Board of Trade in a similar vein, protesting especially against the trade between the northern colonies and the French, which they claimed was in violation of the treaty of neutrality made in 1686 between Great Britain and France.

The matter came to a climax in 1731, when the British planters presented a petition to Parliament with a draft of a bill which would specifically forbid the continental colonies to sell "horses, lumber, and provisions" to any but British subjects (113). Hearings were held on this bill and much evidence was brought out to indicate that the trade in horses was a very important part of this commerce. The testimony of a certain William Fraser is a fair sample of the large amount of evidence in this connection. In 1729 he claimed to have seen about thirty New England vessels at Martinique and St. Lucia trading horses for molasses, and he stated further that the New Englanders told him that if they brought in sixty horses alive they paid nothing for their permission to trade.

The continental colonies vigorously defended their right to trade with the French and the Dutch, and the bill finally failed to pass.[5] A long and acrimonious discussion ensued, finally resulting in the passage of the so-called "Molasses Act," which, by putting a prohibitive duty on the importation of foreign sugar, molasses, and sirups, aimed to put an end to the questioned trade. This act, however, because of the lack of adequate machinery for its enforcement, could not at that time be

[5] An incorrect statement to the effect that such sales of horses to foreign sugar islands were prohibited in 1731 appears in the volume on Rhode Island Commerce, Massachusetts Historical Society, Collections, 7th ser., vol. 9, no. 69, p. 14, note 2.

George II, Chapter 13. This act provided for a duty of sixpence a gallon on molasses and sirups, and five shillings a hundred pounds on sugar imported from any non-American plantation into any British colony. Importations from Spanish and foreign sources were exempted, thus making the act in effect a hindrance only to trade with the French and the Dutch.

made effective — especially since it would have been fatal to a trade which had now become a vital necessity to the continental colonies. It was not until a considerably later time, when the restrictions were revived under Grenville's ministry, that the act really was enforced (114). The trade during the period in question therefore continued practically unchecked, and New England still succeeded in furnishing all the West Indies with horses as well as other supplies.

There is little doubt that during this time horses were a very important source of income to the New England colonies. They are invariably mentioned first among the products of Rhode Island in the reports made by the various governors to the Lords of Trade in London (115). The extent of the shipments is noted also by most of the contemporary writers of the period — "vast quantities of lumber and horses sent out by the New Englanders" (116), as one writer has described it. Some idea of the importance of the trade may be gained also from the complaints of the British planters, already mentioned, because of the supply furnished to their competitors, the French (117). The reports of the governors of New York during this period indicate that this colony also was exporting some horses at this time (118), but not in sufficient quantities to threaten the leadership of New England in the trade.

CONTRABAND TRADE DURING THE FRENCH AND INDIAN WAR

During the years from 1755 to 1763, the period of the struggle between France and Great Britain for supremacy in America, the trade of all the islands of the West Indies suffered more or less. The French sugar planters especially, because of British dominance on the sea, were often in serious difficulties. Nevertheless, plantation supplies continued to be sent out from the continental colonies to both British and French islands. The trade with the French islands was of course contraband, but through various devices it continued to be conducted on a very considerable scale, and by this means French sugar and molasses still found an outlet and the needed supplies were obtained.

Some of this trade with the enemy on the part of the continental colonies was carried on directly under the protection of flags of truce granted by the colonial governors for the ostensible purpose of exchanging

ing prisoners, and in other ways. A very considerable part of the contraband trading, however, was of a more roundabout sort and was effected through the neutral Dutch and Spanish ports. At first the Dutch islands of Curaçao and St. Eustatius were the centers of this trade, but, being broken up in these places by the British fleet, the trade transferred itself to the Spanish port of Monte Christi adjacent to the French settlements on the island of Haiti. Here resorted New England vessels laden with the customary plantation supplies, which they exchanged at very profitable rates for French sugar and molasses in addition to bringing in European goods and taking back part payments in coin (119).

Thus, in spite of difficulties, it was still possible to find an outlet for New England horses, and these continued to be supplied to both French and British planters. This is indicated, for example, by the complaint of Governor Hardy to the Lords of Trade in 1757 to the effect that the New England colonies still continued to send supplies to the enemy. Governor Hardy mentions a privateer "lately come into port which reports having spoke several vessels off Block Island bound for the Indies with horses notwithstanding the general embargo agreed on by the several governors" (120). In 1762 also the British fleet in the Bahamas seized a similar vessel bound for Cayenne with lumber, provisions, and horses (121).

After the conclusion of peace between France and Great Britain in 1763, the commerce between the northern colonies and the British islands went on as before. Between that date and the beginning of the American Revolution, horses were again a considerable item of exchange. In the years 1771 and 1774, according to the record of the Secretary of Customs in London, there were imported into the British islands from "North America" a total of 3647 oxen and 7130 horses (122). The trade with the French islands, however, fell off considerably because of the resurrection of the Molasses Act and the establishment of means for its adequate enforcement, as well as other trade acts that were passed (123).

CHANGES IN THE PRODUCTION OF SUGAR

In addition to the effect of the continued growth of both British and French sugar plantations throughout this period, with the various inter-

ruptions in the trade resulting from wars, acts of Parliament, and other causes, there remained still another factor that affected the demand for horses. This was a change in the methods of manufacture of sugar, which took place in connection with a shift in the center of production from the small islands, such as Barbados, Antigua, and Guadeloupe, to the larger ones such as Jamaica and Haiti.

The advantages of the larger islands for the production of sugar were numerous, and they early became apparent to both the British and the French. In both Jamaica and Santo Domingo there were extensive savannas where pasturage was abundant, and the planters thus were able to produce in some measure the livestock needed for draft purposes on the plantations as well as some to be used for food; in addition both islands were well stocked with wild horses and cattle left from the former Spanish occupation; (124) and, further, there was plenty of timber to be found, of a sort which could be used in constructing sugar mills.[7] In Jamaica, at least, sugar could be cured more quickly than in the islands of the Windward group (125). Another factor probably of more importance than any of the others, was the presence of numerous streams capable of furnishing water power for turning the heavy cylinders of the cane-crushing mills (126). All of these conditions tended to facilitate the production of sugar, and as a result Jamaica and Santo Domingo were enabled to increase their output at a more rapid rate than the small islands could do.

The use of water power for driving the cane mills naturally removed the need for horses and cattle for this task. A similar displacement took place to some extent even in the colonies not possessed of adequate water power. In such colonies resort was had to wind-driven mills and in Barbados, for example, according to Oldmixon, there were by 1741 forty mills of this type to one of the earlier sort (127). On the whole, however, there probably remained in operation a very considerable number of the older horse and cattle mills, and this, together with the fact that they were still needed to haul supplies and to bring the canes from the field, continued to make horses an important item in the

[7] Jamaica was taken by the English from Spain in 1655 and was found to be well stocked with horses and cattle that it was at once proposed to supply the Leeward and the other British colonies from there. This plan was given up, however, because of the difficulty of sailing from Jamaica to the Windward Islands due to the prevailing winds

needed supplies for the sugar plantations. Also, in Jamaica and in Santo Domingo, in spite of their own abundance of livestock, numerous instances are recorded of their continued importation throughout the period (128). Lastly, the demand for saddle horses was a continuous and important one in all the sugar colonies and, further, was a demand which grew with the general increase in the wealth of the planters. In short, it would seem that whatever decrease in the demand for horses may have resulted from the shift in the center of sugar production and changes in the method of manufacture, such decrease was fully balanced by the mere aggregate of the demand from the steadily increasing number of the plantations and the extensiveness of their operations.

Throughout the whole period from 1700 to 1775, therefore, there existed in the West Indies a ready market for horses which was taken full advantage of by the New England colonies, following the beginning already made in this sort of trade before 1700. During the later period, however, the trade was not confined to the British islands, as formerly, but had extended to those belonging to the Dutch and the French as well; it was better organized and on a much more extensive scale; and, though interrupted in various ways from time to time, it had come to be an important part of the commerce of New England and remained so until the War of the Revolution.

DEVELOPMENT OF COMMERCIAL HORSE RAISING FROM 1700 TO 1775

The steadily widening market for horses which was opened up during the period from 1700 to 1775 has just been described. It is apparent also, from the evidence given, that New England took full advantage of the opportunity for exporting horses which was thus presented. There now remains to be considered the resulting development which took place in New England itself during this same period, whereby the raising of horses on a commercial scale became an important industry.

For the beginning of this development no exact date can be set, but certain efforts along this line before 1700 have already been indicated—as for example, the plans of John Hull and his associates in the Pettaquamscut Purchase in Rhode Island. Most of the early shipments of horses to Barbados and the other British colonies prior to 1700, how-

ever, were in the nature of a disposal of an already existing surplus of horses. But with the settlement of Rhode Island and Connecticut these regions soon adopted the raising of horses for export as a regular source of income, and their ports at length came to displace those on Massachusetts Bay as leaders in the trade.

Some of the reasons for the development of the industry in the newer regions have already been indicated. The broader and more level lowlands, extensive salt marshes to furnish hay, lagoons and ponds to serve as natural boundaries for the pastures, all combined to give these regions an advantage. To this should be added the fact that much of this abundant marsh and other forage was easily accessible for boats, which could make their way into the numberless small streams and inlets and there be loaded with little difficulty.[3] This was a matter of no small gain when it is remembered how difficult it would have been to transport such a bulky commodity as hay over the rough frontier roads of the period. Forage of some sort was a very necessary part of the cargo of the vessels carrying horses to the Indies, for the horses must be fed in transit, and the hay, even though it was commonly pressed into rough bales (129), was an unwieldly article to handle; while the horses themselves, if necessary, could be driven long distances to the point of embarkation.

The development of horse raising as an industry in Rhode Island and Connecticut went hand in hand with the development of the commerce of these colonies with the sugar islands. Its extent, however, must mainly be inferred from mention of it in the reports of the various governors to the Lords of Trade in London and from such fragmentary records of actual shipments as are available.

EXPORTATIONS FROM RHODE ISLAND PORTS

The Rhode Island ports were the first in the new region to embark in the export trade, and even as early as 1681 horses are mentioned by Governor Sanford as one of the "principall matters of export" (130). In the next twenty years the shipping had increased "sixfold" and horses were being sent to Jamaica, Barbados, Nevis, Antigua, St.

[3] As early as 1749, hay was being shipped from the region by boat to other ports in New England which were less well supplied. (Elliot, *Essays upon Field Husbandry*, 2d, p. 21.)

Christopher, Montserrat, and Surinam (131). In 1731 Governor Jenks places them first in importance among the exports of the colony, and states that at that time there were ten or twelve vessels engaged in the West Indies trade (132). Ten years later the number of vessels had grown to one hundred and twenty (133). Douglass also confirms the importance to the Rhode Islanders of horses as an article of commerce (134), while the Reverend James MacSparran, for a long time resident in the colony, tells of the "fine horses which are exported to all parts of English America" (135).

Newport and Providence were the main ports of embarkation, but many horses were shipped on small vessels directly from the farms in the Narragansett country (136), where was found the greatest center of the livestock production. In 1745 Moses Brown, one of the more prominent of the Providence merchants, had eight vessels under his management, "some to Surinam with horses" (137); while the correspondence of one Newport firm indicates that during the years from 1731 to 1773 this firm was shipping horses as a regular part of its cargoes to all the British islands and to Curaçao (138).

EXPORTATIONS FROM CONNECTICUT PORTS

At the outset the horses sent out from Rhode Island came into competition with those that continued to be sent from the Massachusetts Bay region, but before long it was Connecticut that had come to be the chief rival in the trade.[9] The renewed enforcement of the Molasses Act after the close of the war with France in 1763 dealt a hard blow to the commerce of Rhode Island, which had been the chief center for the distillation of rum from the molasses received from the French islands,[10] and with the considerable decline in its trade which followed went a lessening of the exportation of horses from its ports and a partial diversion of the trade to the easily accessible outlet at New London in Connecticut, where such shipments had for some time been well established.

[illegible] Newport captain in 1731 quaintly complains to his owners that he has been [illegible] to dispose of his cargo of horses at Antigua because "there was 3 New London [illegible] arrived before I landed. They sold there horses for tow pistoles a head which is [illegible]" (Massachusetts Historical Society, Collections, 7th ser., vol 9 no. 69, p. 16.)

[illegible] the former prohibitive duty of sixpence a gallon was reduced in 1764 to threepence; [illegible] the act was finally repealed in 1766 and a tax of only one penny a gallon was [illegible] ed instead. But between the war and these dates, Rhode Island commerce suffered [illegible]

In addition to those shipped from New London, many Connecticut horses were put directly aboard ship at the towns on the Connecticut river, especially at Windsor, which had a considerable trade with the West Indies (139); and after the middle of the century, considerable numbers were sent out from New Haven. New London, however, was the chief point of embarkation, and many horses, as well as other livestock, were driven in from other colonies to be sent from there to the southern market (140). All the Connecticut vessels were supposed to clear at this port (141), and some of the river vessels undoubtedly took on board their cargoes of horses there (142), although, according to Caulkins, many such vessels "slipped over the bar uncounted" and sailed directly to the Indies (143).

This commerce of the Connecticut coast towns was well known. James Fenimore Cooper, in one of his tales of frontier life written at a date (1832) near enough to the heyday of this trade to have enabled him to get direct testimony as to its extent, puts the following in the mouth of one of his characters: "I have been down at the mouth of both Havens, that . . . named after the capital of Old England and that which is called Haven with the addition of the word 'New' and have seen the snows and brigantines collecting their droves like the ark, being outward bound . . . for barter and traffic in four footed animals" (144).

The Connecticut vessels were mainly sloops and schooners, single-decked and without topmasts; and, unlike those of the other colonies, they were engaged almost entirely in the West Indies trade, making two trips a year. In New London, however, there were built some larger square-rigged ships, with more ample deck space designed to facilitate the transportation of large cargoes of livestock. These "horse jockeys," as they were called, have already been mentioned: one of them sailed from New London in 1716 bound for Barbados with forty-five horses on board, and later others were built which could carry even greater numbers (145). In 1724 six of these ships left port together all freighted with similar cargoes (146), and in 1731 three arrived in Antigua with so many horses as to completely swamp the market (147).

Taken as a whole, the commerce of Connecticut increased very rapidly during this period and continued to increase until the beginning of

the Revolutionary War,[11] and from all the evidence available it is clear that the export trade in horses played no inconsiderable part in this growth. Horses continued to be sent out from Rhode Island and Massachusetts ports, but it was in Connecticut, and especially in New London, that the trade finally came to be mainly centered in the period just before the Revolution.

SOURCES OF SUPPLY FOR THE EXPORT TRADE

Such an extensive exportation of horses from the Connecticut and Rhode Island ports as has just been described indicates the raising of them for this purpose in large numbers and over a very considerable area. Details concerning such horse breeding, however, are very meager. Horses were probably raised to some extent by all the farmers in the region in response to the steady demand that existed.[12] The various cases of horse stealing found in the court records, as already described, as well as the presence of the so-called "horse coursers" who went about the country buying up animals and driving them in herds to the points of shipment, would indicate that this was the case (148).

Here and there throughout the area, however, were certain favorably situated districts where the breeding of horses and of other animals for export was much more specialized. This was the case, for example, on Fisher's Island, just off the mouth of the Thames, which was given over almost entirely to animal husbandry (149). Also, in the Connecticut River Valley the region round about Windsor seems to have been another such center (150). But by far the most extensive and important of these specialized areas was to be found in the Narragansett district of Rhode Island — a region so famed in the annals of the time for its great flocks of sheep, its dairies and cattle, and above all its fine horses, as to have been noted by most of the contemporary writers of the period.

[11] "Between the years 1762 and 1774 the number of Connecticut vessels increased from six, with a total burden of 6790 tons, to one hundred and eighty, with a total of 10317." (Connecticut Archives, Census, p. 5. Cited by Weeden, *Economic and History of New England*, vol. 2, p. 758.)

[12] The inventory of John Walworth, of New London, in 1748 shows the arrangement of the well-to-do farmer's estate of that period. He possessed 4 negro servants, 77 ounces of plate, 50 head of cattle, 812 sheep, and 32 horses, mares and colts (Caulkins, *History of New London*, p. 345).

THE NARRAGANSETT PLANTERS AND THEIR HORSES

Strictly speaking, the Narragansett country embraced all the lands occupied by the Narraganset Indians at the coming of the English; but in the parlance of the time the term came to be applied to a part of this territory consisting of a strip of land about twenty miles long and from two to four miles wide. This extended along the western shore of Narragansett Bay, from Wickford on the north to Point Judith on the south, and thence westward along the coast to include the Champlain tract in Charlestown. It was on this fertile, well-watered plain that there was developed a region of large and pretentious estates—the homes of the Narragansett planters, so called—and here was found a type of agriculture and a social order unlike anything to be found elsewhere in New England.

Channing, who has had access to the local town records of the area and to various manuscripts and family papers, describes these Narragansett planters as follows (151):

> Unlike the other New England aristocrats of their time these people derived their wealth from the soil and not from success in mercantile adventures. They formed a landed aristocracy which had all the peculiarities of a landed aristocracy to as great an extent as did that of the southern colonies. Nevertheless these Narragansett magnates were not planters in the usual and commonly accepted meaning of the word. It is true enough that they lived on large isolated farms surrounded by all the pomp and apparent prosperity that a horde of slaves could supply. But if one looks beneath the surface, he will find that the routine of their daily lives was entirely unlike that of the Virginia planters. The Narragansett's wealth was derived not so much from the cultivation of any great staple like cotton or tobacco, as from the product of their dairies, their flocks of sheep and their droves of splendid horses, the once famous Narragansett pacers. In fine they were large—large for the place and epoch—stock farmers and dairymen.

This region was from the outset one of large-scale agricultural operations. Roger Williams had penetrated the area some time before 1650, and in 1641 Richard Smith had bought a tract of 30,000 acres from the Narraganset sachems and had erected a house (152); but the real settlement of the area did not proceed at a rapid rate until after the Pettiquamscut Purchase (153), made in 1657 by John Hull (the mint-tree shilling fame) and a number of associates, and the Atherton Purchase (154), made two years later by a company headed by Sir Humphrey Atherton and John Winthrop, of Connecticut. Both these groups of owners bent their efforts to obtaining settlers for the holdings. Evidently, because of the many natural advantages of the

tion, they had little difficulty in achieving this result, for in 1670 a letter from Major Mason to the Commissioners of the Colony of Connecticut stated that the land was at that time mainly taken up with farms, some of which were five, six, and even ten miles square (155). John Hull's plan in 1677 for horse breeding on a large scale to get "large and fair horses and mares" for the West Indies trade is noted elsewhere and is another evidence of these large-scale operations. Hull's scheme was a rather ambitious one. He planned to build a stone wall across Point Judith Neck, which would have inclosed a peninsula approximately five miles long and having an average width of about a mile. The object of the wall was to keep out mongrels and strays so that the planters would thus be able to breed up a stock of horses of superior characteristics for shipment to the Indies. Hull goes even further and suggests to his partners, "We might have a vessel made for that service, accommodated on purpose to carry off horses to advantage" (156).

The wealth of the district increased steadily up to the time of the Revolution, and full use was made of the opportunities for animal husbandry of an extensive sort. In 1755 Douglass notes that for New England "the most considerable farms are in the Narragansett country," and that the largest of these "milks 110 cows, cuts about 200 load of hay, makes about 13,000 weight of cheese besides butter, and sells off considerably of calves, fatted bullocks, and horses" (157). In 1747 South Kingston, the center of the Narragansett region, was assessed for the public colony rate a sum only a little less than that for Providence and about half that for Newport (158); in 1780 it had become by far the richest town in Rhode Island, paying double the sum assigned to Newport and two-thirds more than Providence (159). Most of this wealth was apparently derived from agricultural operations.

Their cattle and the output of their dairies were an important source of revenue to the Narragansett planters. But by far the most noted product of the region—at least toward the middle of the eighteenth century—was a breed of saddle horses which they developed.[13] These

[13] preference for pacers appeared at an early date and obviously is the cause of development of the Narragansetts themselves through selection and breeding. The Winthrop writes from Boston in 1684 concerning some horses consigned to him for sale: "I am offered £30 but if the two paced well they would brag nearer £50 such is difference from ordinary jades if they do but pace well" (Winthrop Papers, Massachusetts Historical Society, Collections, 5th ser., vol. 3, p. 446).

were the famous Narragansett pacers, whose praises were sung by all the contemporary writers of the period and tales of whose remarkable performances still linger as part of our American horse lore.

The best description of these unusual pacing horses is given in an article on American agriculture in the first American edition of the Edinburgh Encyclopedia (160), written about 1830 by Robert Livingston. The description reads as follows:

> They have handsome foreheads, the head clean, the neck long, the arms and legs thin and taper; the hindquarters are narrow and the hocks a little crooked, which is here called sickle hocked, which turns the hind feet out a little; their color is generally, though not always, bright sorrel, they are very spirited and carry both head and tail high. But what is most remarkable is that they amble with more speed than most horses trot, so that it is difficult to put some of them upon a gallop. Notwithstanding this facility of ambling, where the ground requires it as when the roads are rough and stony, they have a fine easy single footed trot. These circumstances, together with their being very sure footed, render them the finest saddle horses in the world, they neither fatigue themselves nor their rider. It is generally to be lamented that this invaluable breed of horses is now almost lost by being mixed with those imported from England and from other parts of the United States.

The sturdy qualities of the Narragansett pacers have been perpetuated also by James Fenimore Cooper in his tales of the American wilderness. The horses were evidently still obtainable in Cooper's day (161) and he must have been an admirer of the breed, for he brings them into his stories frequently. They are described by Cooper as being small, sorrel in color, and distinguished by their easy pacing gait and great endurance.

As to the origin of these pacers — the first distinctly American breed of horses — there have been many stories current at one time or another, most of which tales are obviously fanciful. One of the most plausible accounts is a tradition handed down in the Hazard family, of Rhode Island, the early members of which were among the more important breeders of the animals. According to this story the progenitor of the breed was imported from Andalusia, in Spain, by Deputy Governor Robinson (162), whose estate the Hazards inherited.

Wallace (163), a modern writer who has given some attention to the various stories regarding the origin of the Narragansetts, concludes that they resulted solely from careful selection and breeding of the common New England stock. He refuses to give credence to the story

of an admixture of Spanish blood, first, "because there were no pacers in Andalusia or any other part of Spain," and secondly, because "the Narragansetts were a leading article of export from Rhode Island in 1680, thirteen years before Governor Robinson was born." Both these objections made by Wallace are of doubtful validity, however. There is available no such complete information regarding the horses in Spain during the period in question as to justify any such sweeping assertion as to the entire absence of pacers. And, although it is true that horses were reported by Governor Sanford to the Lords of Trade in London in 1680 as an important article of export from Rhode Island, there is nothing to indicate that these horses were of the Narragansett breed. The presumption is that they were not, for the Narragansett district proper was not really settled until about that date. Furthermore, Captain John Hull in 1677 looked on his plan (noted on page 905 for breeding a race of "large and fair horses and mares" as a new venture for the region. In short, the horses mentioned by Governor Sanford were in all probability raised in the northern and eastern parts of Rhode Island, where the country was already in farms before the Narragansett district was settled.

It would seem, therefore, that the tradition concerning the importation of Spanish stock by Deputy Governor Robinson deserves some credence. Whether or not there were any pacers in Spain at the time is immaterial, for it is shown by the correspondence of Governor Winthrop and other writers that pacers were not uncommon in New England as early, at least, as 1684 (164), and the pacing gait of the Narragansetts may very easily be accounted for on the basis of selection and breeding of this native stock. Such selection may have gone on for a greater or less period before the importation of a stallion from Spain to still further improve the breed. Such importation, in fact, is just what might have been expected to happen as attention was increasingly directed to developing an improved strain.

The pacing gait was one of the most characteristic points of the Narragansetts. It is said that the pure-bloods could not trot at all. The gait itself is described as being peculiar in that the backbone of the horse moved through the air in a straight line, thus differing from

that of the common "racker," or pacer of the present day, and from horses having an acquired pacing gait (165). A breed in which the pacing habit was so firmly established must have had back of it an ancestry in which such movement had long been the usual gait. As already indicated (page 894), such a breed is to be found in the Irish hobbies, which were so greatly sought after as saddle horses in England during the early part of the seventeenth century mainly because their pacing gait was easier than that of any other horses of the period. Such fragmentary descriptions of these hobbies as are available (166) disclose a striking similarity in appearance to the Narragansett pacers. These Irish ponies were small, spirited, possessed of unusual endurance, and commonly sorrel in color — all of which characteristics are similarly to be found in the Narragansetts. Although no direct proof can be adduced in support of such a view, it would seem to be at least a plausible theory that the Narragansett pacers resulted from the selection and breeding of some of these Irish hobbies which had been brought to New England at an early date. Later, as indicated by the tradition in the Hazard family, these may have been crossed with some imported Spanish stock to build up the breed still further.

As to the speed and stamina of the Narragansetts and the unusual ease of their gait for saddle purposes, there is much evidence. Pacing races were often held at Little-Neck Beach at South Kingston, and some of the silver tankards won at these races are said by Updike, writing in 1847, to have been still in the possession of some of the old Narragansett families at that time (167). The Reverend James MacSparran, sent out to Rhode Island in 1721 by the Society for the Propagation of the Gospel in Foreign Parts and for many years a resident in the colony, records that he has seen some of these horses pace a mile "in a little more than two minutes and a good deal less than three," and adds further that he has often ridden them "fifty, nay, sixty miles in a day even here in New England where roads are rough, stony and uneven" (168). Another contemporary writer describes "the natural pacers of horses which at a cow run — a gait which they acquire by pasturing when colts with the cows [truly a surprising theory!] will pace three miles in seven minutes."

Further evidence of the unusual ease of the saddle gait of the

Narragansetts is given in a letter written about 1847 and quoted by Updike (169) in his *History of the Episcopal Church in Narragansett*. This describes how in 1791 an aged lady then living in Narragansett rode one of these pacers on a lady's side-saddle to Plainfield, a distance of thirty miles, rode the next day to Hartford, forty miles, staid in Hartford for two days, then rode forty miles to New Haven, then forty miles to New London, and then home to Narragansett, forty miles more. The lady claimed to have experienced no sensible fatigue.

Because of the export trade with the West Indies, horses of any sort would have been a valuable source of revenue to the Narragansett planters,[14] and it is probable that many of the ordinary New England stock were bred for this purpose in the region. But the cream of the demand from the sugar planters was for saddle horses for personal use, and for these they were willing and able to pay extravagant prices. To this demand was added that of persons of means throughout all New England and the other continental British colonies as well.[15] Thus, in these unusual pacers, whose gait and general characteristics suited them so admirably to such use, it is clear that the Narragansett district had a very important source of revenue and one which probably contributed in no small measure to its prosperity.

The horses and other livestock of the Narragansett district designed for exportation to the West Indies found an outlet through the various ports on Narragansett Bay, or were driven to New London or Stonington over the old Pequot trail, which had become the post road between Boston and New York and which passed through the center of the region. Apparently many animals were shipped also directly from the Narragansett country itself; Robert Hazard, for example, is said to

[14] From the account book kept by Thomas Hazard, one of the wealthiest and most prominent of the Narragansett planters, may be gleaned some idea of the prices received. In 17[illegible] he sold a three-year-old at £150, and the next year a thirteen-year-old bay "with a white nose" brought £70; while in 1755 a "black trotting mare" brought only £5. In 1763 a black mare sold for £244, but by that time the Rhode Island currency had greatly depreciated in value and Mr. Hazard noted alongside that £7=1 Spanish Milled Dollar." In 1766, however, one "dark colored natural pacing horse with some white on his face" brought the high price of fifty-five Spanish milled dollars. (*Thomas Hazard, Son of Robt., call'd Collector Tom*, p. 63.)

[15] Watson (*Annals of Philadelphia and Pennsylvania*, p. 209) gives an account of one such shipment in 1711, as recorded in a letter written by a certain Rip van Dam who engineered the transaction on behalf of Jonathan Dickinson, of Philadelphia. The horse was shipped from Rhode Island in a sloop, from which he jumped overboard and swam ashore to his former home. Recaptured, he finally arrived in New York, fourteen days passage much reduced in flesh and spirit." He cost £30 plus 50 shillings for freight, and was evidently an animal of spirit; he "would not stand still two days about all the time;" he would "drink a glass of wine or beer or cider," and van Dam further opines that "he would drink a dram on a good cold morning."

have raised about two hundred horses annually and to have loaded two vessels a year with them and other produce of his farm. These vessels sailed "from the South Ferry directly to the Indies where the horses were in great demand" (170). It was the Hazard family[16] which seemed to have been mainly concerned in the early development of the Narragensett pacers, and it is probable that many of the horses thus shipped were of the famous breed.

To recapitulate, then, it may be said that during this period from 1700 to 1775, in response to the demand from the West Indies sugar plantations for draft animals and from the same source and from all the continental colonies for saddle purposes, the breeding of horses finally became, in the period just preceding the Revolution, a widespread industry throughout all Rhode Island and Connecticut and probably in the other New England colonies as well and that in some particularly favored spots it was carried on in a highly specialized and extensive fashion. The "horse jockeys" with their large cargoes, the numberless small vessels carrying only a few animals on their scanty decks, the famous pacers driven overland to neighboring continental colonies, all must have contributed a very considerable item of revenue to the New England region and aided the colonists in that search for "a good return" on which they were always bent.

DECLINE IN HORSE RAISING AFTER THE REVOLUTION

The exportation of horses, which was interrupted during the Revolution as was the other commerce of the colonies, was revived at the close of the war. Now, however, the New England vessels were denied entrance to the British sugar islands by the decree restricting trade to British bottoms, so that a considerable proportion of the former outlet for horses no longer existed. Such shipments as were made went mainly to the French islands and to Cuba, which by this time had been thrown open to trade by the Spaniards and was developing rapidly as a producer of sugar.

This revival of the horse trade seems to have had its main [illegible] in New London. The "horse jockeys" were once more embarked [illegible] their former service; one brig took out forty-nine horses, and many [illegible] coops

[16] The Robert Hazard mentioned above was born in 1689 and died in 17[illegible]

carried as many as thirty-five in a single cargo. The *Enterprise,* bound for Demerara, carried provisions, brick, lumber, twenty horses, seventeen neat cattle, and seventeen mules, besides swine, geese, and turkeys (171). The general extent of these shipments is shown in a marine list kept by Thomas Alden in the *New London Gazette*. According to this record there was sent out from New London during the year 1785 a total of 8094 horses and cattle; and in the years following, the numbers were, successively, 6671, 6366, and 6678 the record ceasing with the year 1788 (172).

This revival of horse exporting apparently was not especially successful and did not continue long,[1] for the New London vessel owners were soon casting about for some better occupation for their ships. On the return of two of these ships from an expedition to the Gulf of St. Lawrence with profitable cargoes of whale oil, the *New London Gazette* exhorts, in rather mixed metaphor, "Now my horse jockeys, beat your horses and cattle into spears, lances, harpoons and whaling gear, and let us strike out" (173).

The reopening of the British West Indies ports to New England vessels in 1789 (174) apparently failed to halt the decline that had begun in the New England horse trade, if one is to judge by the infrequency with which this trade is now mentioned. It is probable that in the general interruption of the trade during the Revolution, the sugar islands, thrown on their own resources, had learned to furnish their own supply (175). As already indicated, the larger islands of Jamaica and Haiti were plentifully supplied with pasturage and wild horses by means of which this could be accomplished. Nor was Cuba as promising a market as might have been expected, for it possessed similar advantages. In addition, the substitution of water power for the mills probably continued to take place in all the islands where it was possible. Lastly, there are indications that the pasturage available in New England itself was not so ample as formerly and was being

[1] An indication of the general decline in the exportation of horses which occurred after the Revolution is found in the following table reproduced from Pitkin (*A Statistical View of the Commerce of the United States of America* p. 62 633). These figures include shipments from other ports besides those in New England

Year	1791	1792	1793	1794	1795	1796	1797	1798
Horses exported from United States	6,975	5,656	3,728	3,495	2,626	4,883	1,177	2,132

gradually infringed on by the cultivation of new land; in fact, according to Elliot (176) this scarcity of pasture land and meadows, with the resultant high price of hay, had begun to be felt even before the Revolution. All these things combined to make difficult the resumption of the trade in horses on its former scale.

Just what became of the large number of animals which had for so long furnished a steady article of commerce is not very clear. The very considerable shipments to the French islands, already noted, which immediately followed the close of the Revolution, probably accounted for such surplus of the ordinary stock as had accumulated; while the demand for saddle horses on the part of the increasingly prosperous Spanish planters of Cuba probably took many of the Narragansett pacers (177). Then, too, the mere cessation of breeding new colts, as the demand for export purposes lessened, would have had an immediate effect on the numbers. But most important of all, doubtless, was the breaking up of former pastures for the purpose of cultivating field crops to supply the demand of Europe for provisions during the war between France and England which began in 1793 and which soon forced prices for such supplies to a high level. The effect of such a change in agriculture would be, on the one hand, to cut down the number of horses that could be cheaply raised, and, on the other, to give ample opportunity for the employment in the new operations of the horses already available. Finally, as the people from New England pushed westward to the settlement of newer lands in New York and elsewhere, they also probably drew off considerable numbers from the existing supply.

Another event indicating the changed conditions in horse raising as a New England industry during this period following the Revolution, was the disappearance of the Narragansett pacers. This breed, so carefully developed and so noted in the annals of the time, at length became extinct and is known at present only as a sort of legendary strain whose connection with other American breeds, if any connection exists, is mainly a matter of conjecture.

The demand for the Narragansetts from the wealthy planters Cuba, when that island at length began to cultivate sugar extens has been assigned by one writer (I. P. Hazard) as the chief cau of the disappearance of the breed. He says in part: "The planter became suddenly rich and wanted pacing horses . . . to ride, fa than

we could supply them, and sent an agent to this country to purchase them on such terms as he could . . . He commenced buying and shipping till all the good ones were sent off" (178).

It is easy to understand that such a large and unexpected demand from Cuba, without restriction as to price, might deplete the breed very seriously. But if the Narragansett planters did thus actually kill the goose that laid the golden eggs by shipping off all their breeding stock, it must be that there were other factors at work which made them willing to sell. It might indicate, for example, that their experience in attempting to sell in their former markets after the war, had convinced them that the end of the earlier export trade was in sight.

There are, however, other obvious reasons which probably contributed to the dispersal of the sturdy little pacers which had so long been a profitable commodity. They were not beautiful at best; they were small, scarcely more than fourteen hands high, and their gait, while desirable for saddle purposes, did not fit them for driving to advantage in team or harness (179). All these things undoubtedly worked against the Narragansetts as the roads in the colonies became better, wheeled vehicles came into use, and there was need for larger and heavier animals for harness and draft. The pacers were, in short, of most value under frontier conditions, and as the region along the coast became more settled there is evidence that they were actually dispersed to remoter regions, especially to Canada, Kentucky, and Tennessee. It is in these places that the pacing blood seems to have been preserved in the midst of the influx of English thoroughbred stock beginning about 1750 (180).

Thus closed the final chapter in New England's leadership in the exportation of at least one product of an agricultural nature — a leadership which had been held undisputed for more than a century; which in the [illegible] years of her early commerce had eked out to good purpose the exchanges of New England with the West Indies and by which she was enabled in turn to purchase English goods; which had aided in the [illegible]ning and settlement of her lands remote from the coasts and harb[illegible]; and which finally had a part in the development in the Narragans[illegible] district of a social and economic organization based on agricult[illegible] which was comparable to any other found in continental Am[illegible] during the colonial period.

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Memoir 52, *Studies in Pollen, with Special Reference to Longevity*, was mailed on March 9, 1922.

MAY, 1922 MEMOIR 55

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

INSECTS AND OTHER ANIMAL PESTS INJURIOUS TO FIELD BEANS IN NEW YORK

I. M. HAWLEY

ITHACA, NEW YORK

PUBLISHED BY THE UNIVERSITY

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INSECTS AND OTHER ANIMAL PESTS INJURIOUS TO FIELD BEANS IN NEW YORK

INSECTS AND OTHER ANIMAL PESTS INJURIOUS TO FIELD BEANS IN NEW YORK

I. M. Hawley

In June, 1917, a laboratory was established at Perry, in the bean-growing section of western New York, for an investigation of the diseases and the insects that had been causing much injury to field beans. In this work the Departments of Entomology, Plant Breeding, and Plant Pathology at Cornell University were each represented by one member. This investigation has been carried on for four years, and the results, on the whole, have been satisfactory. The entomological work, however, has been hindered by one unavoidable circumstance: in some summers the insect pests under investigation were very scarce, and field experiments for their control were thus impossible. As a result, the recommendations in some cases are based on fewer data than the writer had wished.

The more important part of this investigation is the part concerning the seed-corn maggot (*Hylemya cilicrura* Rond.). The field gray slug *Agriolimax agrestis* L.), a mollusk of the family Limacidae, also has been studied in detail, and some attention has been given to the green clover worm (*Plathypena scabra* Fab.), the red-headed flea beetle (*Systena frontalis* Fab.), the pale-striped flea beetle (*Systena taeniata* Say), the blue-banded millepede, or thousand-legged worm (*Julus caeruleocinctus* Wood), and the bean weevil (*Acanthoscelides obtectus* Say). Observations were made also on the habits of some insects of lesser importance, in particular those that produce the pitting of the bean known as *dimpling*.

THE SEED CORN MAGGOT

(*Hylemya cilicrura* Rond.)

It is difficult to obtain exact data concerning *Hylemya cilicrura*,[1] for it is an erratic insect that may occur in a field in great numbers in one season, and not reappear in, or even near, that field the following year. The flies usually disappear in late summer and the hosts of the larvae during that part of the year are not definitely known. Reared flies apparently do not mate in captivity. Infestations of the insect in cultivated crops are not usually found until considerable damage has been caused. By that time the maggots are full-grown and it is too late for control experiments with that brood. The writer realizes the many gaps in the present work, but, as the insect is scarce at the present time, it seems desirable to record the results thus far obtained.

[1] This species is more commonly known in American literature on economic entomology as *Phorbia fusciceps*.

SYSTEMATIC POSITION

The parent insect of the seed-corn maggot (*Hylemyia ciliicrura*, Plate LXIX, 1) is a fly of the order Diptera and the family Anthomyiidae. The insect was first described by Rondani (1866)[2] as *Chortophila ciliicrura*. Until recently, however, *ciliicrura* has been considered synonymous with *fusciceps* of Zetterstedt (1845), and, since Zetterstedt's description precedes that of Rondani, *fusciceps* has been accepted as the specific name of the insect. Stein (1916) finds that *fusciceps* is a distinct species and not the *ciliicrura* of Rondani. Malloch (1920) accepts the separation of the two species made by Stein. The species *fusciceps* of Zetterstedt occurs in Lapland and other parts of northern Europe, and recently Malloch (1920) has recorded it from North America. The species *ciliicrura*, in addition to a wide European distribution, is present in most parts of North America, and is the pest known as the seed-corn maggot. The *fusciceps* described by Slingerland (1894) is not the *fusciceps* of Zetterstedt but is *ciliicrura* Rond.

Stein (1916) places *ciliicrura* in the genus Chortophila, but Malloch (1920) unites the genera Chortophila, Phorbia, and Hylemyia in the strict sense, in the genus Hylemyia. If we follow this latest paper on the subject, the seed-corn maggot must be called *Hylemyia ciliicrura* Rond.

In the recent European writings of Reh (1913) and Oberstein (1916), the specific name *Chortophila ciliicrura* is applied to this insect; but in older works, such as that of Ritzema Bos (1890), mention is often made of *Anthomyia platura*. The species *platura* is a composite of *ciliicrura* and *trichodactyla*, and often it is impossible to determine definitely which species was blamable for the work these authors have described.

COMMON NAMES

The common names given to *Hylemyia ciliicrura* include the following: deceiving wheat fly, locust-egg anthomyian, Anthomyia egg parasite, seed-corn maggot, corn Anthomyia, seed-corn flower-fly, bean maggot, bean fly, fringed anthomyian. Of these, the name *seed-corn maggot* is the best known and is the one retained in this paper.

HISTORY

Hylemyia ciliicrura is probably of European origin. In North America the first record was that of Fitch (1856), who found the fly on wheat heads and described it under the name *Hylemyia deceptiva*. Riley (1869) discovered the larva attacking corn in New Jersey and named the fly *Lithomyia Zeae*, but nine years later (Riley, 1878) he called it *Anthomyia cilicrura* Meigen when he found the maggots feeding on locust eggs in Kansas and other western States. It was reported that ten per cent or more of

[2] Dates in parenthesis refer to *Bibliography and Literature Cited*, pages 1025 to 1037

these locust eggs were destroyed in this way. Later, Jack (1886) found the maggots destroying field beans in Canada. At intervals since that time the pest has suddenly appeared, destroying bean seedlings and injuring many other crops both in the United States and in Canada.

During the last few years *H. cilicrura* has once more become active in the New York bean fields, after a period of scarcity covering many years. Since 1914 moist weather conditions have tended to augment the normal number of flies. The injuries caused by the maggots of this species reached a maximum in 1917, but since that time there has been a gradual decrease in the amount of damage, and in 1919 and 1920 the loss due to the insect was hardly noticeable.

DISTRIBUTION

The seed-corn maggot has been found in many parts of the United States and Canada. It has been reported from nearly every State, from Maine to Florida and westward to the Pacific. In Europe, reports of its presence in Austria, Germany, Italy, England, and France may be found. It has been reported also from Hawaii.

Chittenden (1916) states that the species *cilicrura* causes much of the loss in the States south of New Jersey which is credited to the cabbage maggot, *Hylemyia* (*Phorbia*) *brassicæ* Bouché, and to the onion maggot, *Hylemyia antiqua* Meigen (*Phorbia ceparum* Meade). Chittenden believes also (1909) that some of the work on the Pacific Coast attributed to *Hylemyia planipalpis* Stein may be due to *H. cilicrura*.

FOOD PLANTS

Hylemyia cilicrura has a wide range of food plants, according to Chittenden (1902) and other writers. Among the commoner of these may be mentioned beans, peas, lettuce, corn, cabbage, cauliflower, beets, turnips, radishes, seed potatoes, sweet potatoes, domestic garlic, crimson clover, onions, and hedge mustard. Whelan (1916) reports the maggot as breeding in fresh manure, in clover and alfalfa sod, and in rotting clover stems. Tucker (1917) reports *cilicrura* injury on tomatoes and cauliflower, and says that the larvae were found developing in decomposed cotton seed. Garman (1904) found the insect in young hemp plants. Pettit (1910) mentions pumpkin, cotton, orange, artichoke, and strawberry as hosts. Parks[1] bred *cilicrura* from maggots in the "bulbs" of wheat. Howard (1900) states that the fly has been bred from human excrement. Riley (1878) found the maggots feeding on locust eggs.

The attraction of the insect for decaying matter has been recognized by many writers. Chittenden (1902) cites, as an example of this, the finding of the larvae in tineid galls on poplar trees. Quaintance and Jenne (1912) found the flies appearing in cages where decaying plums

[1] Quoted in a general discussion reported in the *Journal of Economic Entomology*, vol. 9, p. 133, 1916.

were used in rearing the plum curculio. Johannsen (1911) thinks the species is attracted by decaying matter in the soil. Berger (1908) found the insect working in cut surfaces of seed potatoes that showed decay. Schoene (1916) has often bred the insect on cabbage, and believes the species is attracted to that plant by decomposition in parts of it. Blackman and Stage (1918) bred the species on a decaying root of larch.

The insect has been reported also in Europe. It was found on sea kale in England, and Ritzema Bos (1890) reported finding the species *platura* (which, as already noted, is a composite of *cilicrura* and *trichodactyla*) on human excrement, on asparagus, on leek (*Allium porrum*), and on shallot (*A. ascalonicum*). More recently this species has been discussed, under the name *Chortophila cilicrura*, as a pest of rye and corn in Silesia (Oberstein, 1916). Kornauth (1916) reports *trichodactyla* as injurious to beans in Moravia.

Under field conditions in western New York during the progress of the present study, larvae of *Hylemyia cilicrura* have been found in beans, peas, corn, seed potatoes, and alfalfa roots. Baits of decaying materials were placed near the laboratory, and later examination showed the following to contain maggots: cabbage, bean pods, bean vines, grass stems, clover roots, and clover stems. Two larvae have been found in mustard growing near a bean field, and two flies were bred from larvae taken in late summer in the roots of quack grass (*Agropyron repens*). The species has been reared also from pupae found in a pile of rich soil that had been taken from beneath decaying stumps. The writer has never bred the fly from manure.

From these data it may be seen that the list of known hosts is both large and varied, including not only healthy and decaying vegetable tissue, but also animal tissue. It is probable that this list is far from complete.

The first flies taken each spring have been found by sweeping old wheat fields, and the writer believes that wheat, oats, and possibly other grains may constitute important late-season hosts; but as yet sufficient data are not available for proof of this. Mature females of the second brood, taken in July, were numerous near sod and quack grass, and these also may be common winter hosts of the insects.

NATURE OF INJURY TO BEANS

The larvae of the seed-corn maggot may feed on three parts of a bean seedling—the plumule, the cotyledons, and the radicle. The injury to each part of the plant is here discussed separately.

Injury to the plumule

When the small larva locates a source of food in a sprouting bean it usually crawls between the cotyledons, or seed leaves, and feeds on the two leaflets of the plumule and on the small bud of the growing tip between

them (Plate LXIX, 4, and fig. 86, A). This vegetative part of the plant may be entirely eaten away so that when the seedling comes above ground

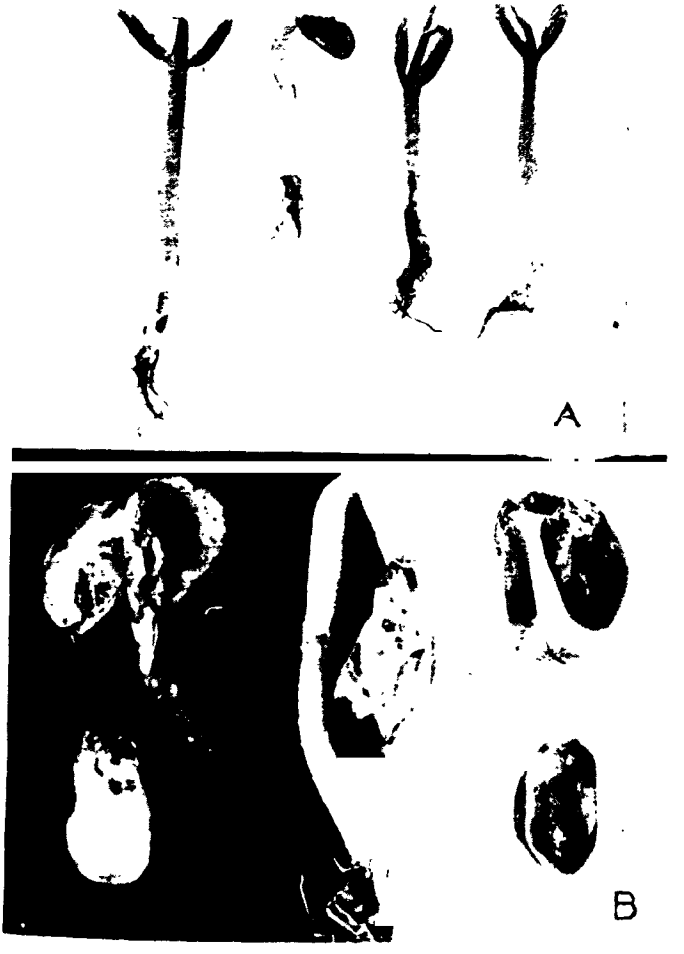

FIG. 86.—INJURY BY HYLEMYIA CILICRURA

A, Types of injury in bean seedlings. B, Injured bean plants known as *snakeheads*, showing the result of feeding by the seed-corn maggot

only the cotyledons remain. This stunted form of plant is known to bean growers as a *snakehead*, or *baldhead* (fig. 86, B). Usually a snakehead shrivels up and dies, but occasionally one succeeds in producing accessory

buds and in developing leaves and a few flowers (fig. 87, A). At harvest time a plant of this type is found to bear few if any pods and is still a dwarf plant (fig. 87, B). The formation of snakeheads is the severest form

FIG. 87 RESULT OF WORK OF HYLEMYIA CILICRURA, AND EGGS AND ADULT [illegible] OLIMAX AGRESTIS

A, Snakeheads putting out a new growth of small leaves. B, Two bean plants in late [illegible] one on the left came from a snakehead, while the one on the right is a normal plant [illegible] C, Eggs deposited in the soil by *Agriolimax agrestis*, [illegible]. D, The field gray slug [illegible] slightly reduced

of injury to the bean caused by the seed-corn maggot, and in some fields the writer has found 75 per cent of the plants to be thus deformed.

If the maggot feeds on the leaf tissue of the plumule but does not destroy the growing tip, a thrifty plant may still result. The first two leaves may be misshapen and ragged, but new leaves are soon produced to take their places.

Injury to the cotyledons

Often a larva does not injure the cotyledons until it has fed on the plumule. Its entrance into a cotyledon is thru a hole made in the side, and the maggot usually hollows out the fleshy interior until little more than a shell remains. The maggots are often carried above the ground concealed in the cotyledons, and a single plant may have eight or even more hidden in these two seed-leaves. Damage to the cotyledons alone is not a serious handicap, as these are of little use to the plant after the true leaves have been formed.

Injury to the radicle

When a seed germinates so quickly that the cotyledons are pushed above the ground before any maggots locate the plant, the radicle may be attacked. The larva makes a small hole for its entrance and then mines upward thru the fleshy tissue of the stem. This injury is not serious, as the course of the maggot is thru the pith and it seldom disturbs the vascular tissue. In 1917 the writer observed a field near Batavia in which the beans were planted very deep. Soon after planting, a period of dry weather baked the top soil solid. The beans grew until they reached this upper impenetrable surface layer, and then they were bent over. Many maggots were found in the stem of each plant.

LOSS CAUSED

The year 1917 was a serious one for New York bean growers, because of the continued rains and the prevalence of maggots during the planting time, in June. In five townships of Genesee County the loss of seed attributed to *Hylemyia cilicrura* was estimated at $15,000. In Erie County the loss on 10,478 acres was said to be 40 per cent. In Monroe County from 50 to 75 per cent of the beans on 16,000 acres were destroyed, while in Orleans County one-fourth of $96,000 worth of seed was wasted. Many growers had to plant their beans two or three times, and one grower, who reseeded twice before getting a stand, estimated his loss for seed at $300. Similar injuries to bean crops were reported from New Jersey, Pennsylvania, Michigan, and Canada. At intervals in the past this insect has appeared thus suddenly and unexpectedly, has seriously damaged beans, corn, and other crops for a few subsequent years, and has then gradually disappeared for a time.

DESCRIPTION OF STAGES

The egg

The chorion, or outer covering, of the egg (figs. 88 and 89, C) is white, glistening, and marked with longitudinal furrows. Similar cross-furrows connect the longitudinal ones, cutting off irregular areas about twice as long as their width. One end of the egg is rounded and the other is rather bluntly flattened. Two prominent ridges, starting at either end of the flattened part, meet at a point about one-fourth the length of the egg. When the larva emerges, the chorion splits near these ridges. The length of the egg is about 1 millimeter (1 25 inch).

FIG. 88. EGG OF SEED-CORN MAGGOT, × 30

The larva

The full-grown larva (Plate LXIX, 2, and fig. 89, D) is white, and is largest at the caudal end, tapering anteriorly. In the early stages it is slender and almost conical, but as it nears the time for pupation it becomes shorter and almost elliptical in form. The first segment bears a pair of black, hooked jaws which may be extended and retracted. The anterior spiracular process is heavily chitinized and bears six or seven lobes. The posterior spiracles are small and consist of three slitlike openings with toothed edges. These spiracles, which are the external openings of tracheae running lengthwise thru the body, may be found on the flattened caudal end of the larva. This flattened, almost truncate, segment bears seven pairs of fleshy tubercles. The length of the larva is from 6 to 7 millimeters ($\frac{1}{4}$ inch).

The puparium. The puparium (figs. 89, A, and 90) is brown in color and elongate-oval in outline. The puparium is the cast skin of the last molt of the larva, and so shows many larval characters. The anterior spiracles are present on the anterior part of the puparium and still show six or seven lobes. The fleshy tubercles on the caudal end of the body also remain but are less prominent. The length of the puparium is about 4 to 5 millimeters ($\frac{1}{6}$ to $\frac{1}{5}$ inch).

The adult

The male (Plate LXIX, 1, and fig. 89, B). The body color of the adult male is greenish gray, with the legs darker and the antennae black. The entire body bears many black bristles. Faint dark lines run lengthwise on the dorsum of some specimens, and a prominent black line runs along the middle of the dorsal side of the abdomen. The main distinguishing character of the species is a row of regularly arranged bristles on the tibia of the hind leg (Plate LXIX, 3). This separates the species from

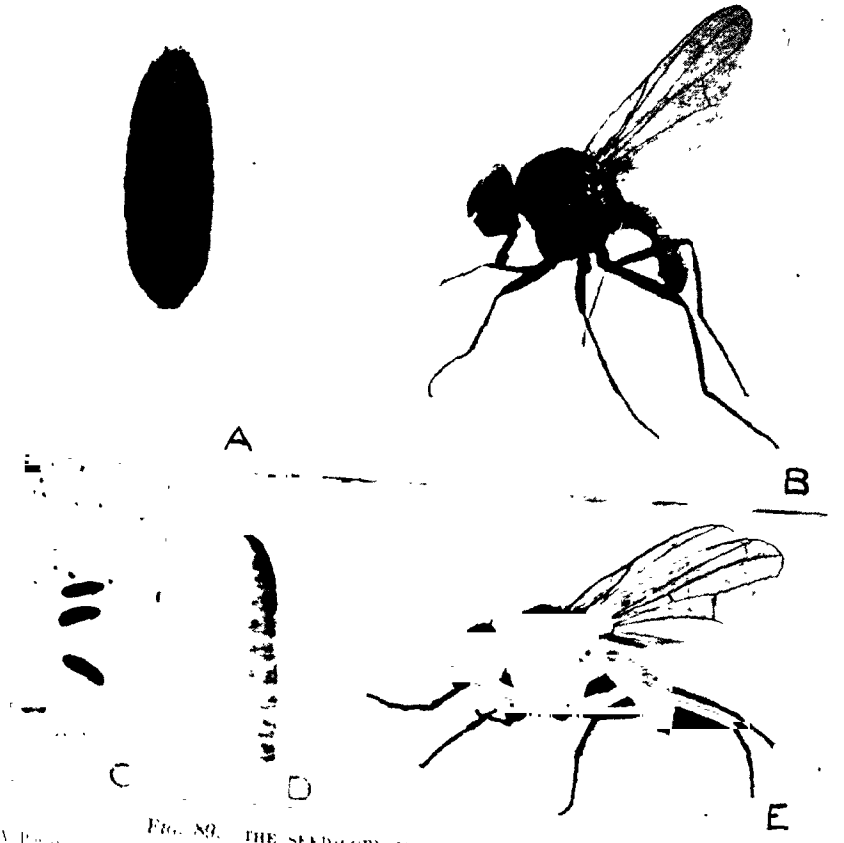

FIG. 89. THE SEED-CORN MAGGOT, HYLEMYIA CILICRURA

A, Puparium, × 5. B, Parent fly, male, × 10. C, Eggs, enlarged. D, Larva, × 5. E, Parent fly, female, × 10.

from *brassicae* and *antiqua* (*coparum*), with which it is often found associated in the field. In *brassicae* there is a tuft of fine setae at the base of the femur, which is lacking in *cilicrura*. In *tuchedactyla* the middle metatarsus bears long hairs on the upper side, which are lacking in *cilicrura*. The length of the adult male of *cilicrura* is about 5 millimeters (¼ inch).

The female (fig. 89, E). The female of *cilicrura* is similar to the male, but

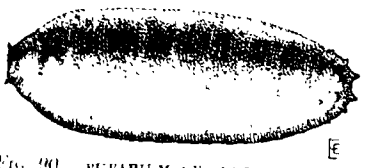

FIG. 90. PUPARIUM OF SEED-CORN MAGGOT, × 5½

the abdomen is pointed instead of rounded and the bristles on the body are fewer and shorter. The female lacks the prominent fringe of hairs found on the tibia of the male, and is harder to distinguish from related species. In *brassicae* the pre-alar bristle is as strong and as long as the first dorso-central one, while in *cilicrura* and *antiqua* it is only about half as long. In *antiqua* there are two nearly equal setae on the anterior (outer) side of the middle tibia, while in *cilicrura* there is usually but one. The species *antiqua* is ordinarily larger than *cilicrura*. The length of the female of *cilicrura* is 5 millimeters ($\frac{1}{5}$ inch).

LIFE HISTORY AND HABITS

The egg

There is little in the literature regarding the egg-laying of *Hylemya cilicrura*. Whelan (1916) reports that the fly usually places its eggs either on the stems of plants just as they come thru the soil, or on decaying vegetable matter. Howitt (1911) states that the eggs are deposited on decaying matter in the soil. Lugger (1896) was able to bring about the deposition of eggs by flies in captivity, but he believed the eggs to be sterile for he failed in his attempts to rear flies from them. Chittenden (1909) mentions an instance in which decomposing crimson clover that had been plowed under attracted flies as a place for oviposition.

Period of incubation

In July, 1917, at Perry, New York, the length of the egg stage under very moist conditions was between 24 and 48 hours. Very few eggs were found and the exact time of oviposition was in doubt.

In 1918 eleven first-brood eggs under observation hatched in an average of 66 hours, as shown in table 1. There was a wide variation, from 41 to 91 hours, and many eggs, the exact hatching time of which could not be noted, hatched within these limits. Eggs were kept in petri dishes on moist blotting-paper or damp earth.

TABLE 1.—LENGTH OF THE EGG STAGE IN 1918

Number of eggs	Time of deposition	Time of hatching	Length of stage (hours)
3	May 23, 3 p. m.	May 27, 9:30, 10, 10, a. m.	90.5, 91, 91
4	May 25, 4 p. m.	May 27, 9, 10, 10, 11:30, a. m.	41, 42, 42, 43
4	May 25, 3 p. m.	May 28, 9:30, 10, 10:30, 10:30, a. m.	70.5, 71, 71, 71.5

Average, 66 hours

In 1919 notes were taken on the period of incubation of 28 eggs on moist earth. The average for these was 2.8 days, with a range from one to five days. Four eggs kept on dry blotting-paper in a petri dish required between three and four days. One egg, deposited on June 4, did not hatch until June 17, but this is the only instance of so long a period of incubation.

Place of oviposition

The insect is strongly attracted to moist and decaying material as a place for oviposition, but under some conditions the flies will place their eggs on dry material, as the following experiment shows. On June 4, 1919, many flies, taken by sweeping, were placed in a cage with a flower-pot containing dry bean stems and dry soil. This pot was kept dry until the flies died, after which it was moistened in order to see whether a new lot of flies would develop. On July 3 one fly was found in the cage, and on July 8 two more were found. In another cage the same conditions prevailed except that the jar was moist during the entire experiment. Four flies were found in this cage on July 3, and eight more on July 8.

In the field, eggs have been found around decaying bean pods and vines and around rotting cabbage. The writer has spent a great deal of time in looking for eggs on freshly plowed ground where mature flies were seen in large numbers, but has succeeded in finding only a few in such locations. Two eggs were found on newly turned soil and one was discovered in a crevice in a recently disked field. Egg-laying was induced by throwing water on the parched and cracking ground near the laboratory at a time when the flies were numerous. Eight eggs were found on top of the ground in one of these spots within two hours after it was thus moistened, and, in all, about one hundred eggs were obtained in this way.

Whelan (1916) says that the maggots of *H. cilicrura* are sometimes found in fresh manure. The writer, however, has not seen the larvae in manure, nor has he been able to bring about oviposition on manure. On June 5, 1919, flower-pots containing fresh cow, horse, hog, and hen manure were placed in a cage containing many adults of *cilicrura* that had been taken in the field. When these pots were examined later, no eggs could be found, and no flies ever emerged in the cage. On June 3, 1919, flies were placed in a large cage containing one flower-pot of manure of different kinds and another filled with decaying bean vines and grass sod. After the flies were all dead, the pot of manure was moved to another cage. No flies emerged from this pot. In the cage containing the pot with the decayed beans and grass sod, thirteen flies emerged. This apparently shows the insects' preference for decaying beans and clover rather than for animal manure, as a place for oviposition. Many times fresh manure found in fields where the flies were abundant has been placed in cages, but no flies have ever emerged. Furthermore, the flies have not been found in abnormal numbers around either manure piles or fresh manure dropped along the road.

Is it possible that manure has an attraction for the maggots developing from eggs deposited in the soil, which leads them to use it as a secondary host?

In cages, eggs of the first brood have been found singly as a rule, tho they have been found occasionally in groups of from two to five, in some cases side by side and in other cases piled on one another irregularly. When first-brood flies taken in the field were placed in cages, eggs were deposited on decaying mustard stems, on stems and roots of grass, on old bean pods and vines, and on cabbage stumps. Some eggs were found also on the surface of the ground, and some in the top inch of dirt. A few were attached to the side of the flower-pot, both above and below the soil line. Eggs of the second brood were deposited by flies in captivity on top of the soil and in the dirt itself.

Number of eggs

The writer has not been able to bring about oviposition by flies reared in captivity, and accordingly he could not determine the exact number of eggs deposited by a single female. The following may be mentioned as typical examples of many dissected specimens. On May 27, 1918, 87 eggs, of which 25 were almost fully developed, were found in a dissected fly. On May 15, 1919, two flies were found with nearly mature eggs, one containing 30 and the other 48. In 1920 two flies were found containing 83 and 64 eggs, respectively, on May 7; and on May 19, five flies contained, respectively, 56, 25, 37, 85, and 72 eggs. It is believed that all the eggs in an insect mature at about the same time and that oviposition is completed within a few days. From these data it seems possible that a female may deposit 80 or more eggs, but the number may often be much smaller.

Time of oviposition

Since it is from the eggs of the first brood of flies that the maggots so injurious to growing crops are produced, special study has been given to this generation. Very little is known of conditions in 1917, as life-history studies did not begin until June 22. In 1918 adults were found containing well-developed eggs on May 9, and, tho some eggs were no doubt deposited by May 15, most of the eggs of the first brood were deposited between May 23 and June 1. Eggs of the second brood were deposited during the first half of July.

In 1919 eggs of the first generation were mostly deposited from May 20 to June 15, with the maximum deposition occurring about June 1. [illegible] second-brood flies were ready to oviposit between June 25 and July 4. [illegible] since a few flies were captured on September 13 and 15 whose abdomens contained immature eggs, it seems possible that a few eggs may have been deposited as late as October. However, these flies may hibernate, which would explain why a few flies with well-developed eggs are found in early May, several weeks ahead of most of the first brood.

The season of 1920 varied little from the two preceding years. The first flies were found on May 7, some containing eggs that were partly developed. Most of the eggs of the first brood were deposited during the first week of June. Eggs of second-brood flies were deposited early in July. The relationship between the time of oviposition and the dates of bean planting is discussed later (page 972).

The larva

Length of larval stage

The average length of the larval stage for eight specimens of *Hylemyia cilicrura*, which had been bred in vials in a field cage at the Perry laboratory in 1917, was 10.4 days, with a variation from 8 to 12 days. The data are given in table 2:

TABLE 2 BREEDING DATA FOR EIGHT FLIES REARED IN 1917

Date of hatching	Length of larval stage (days	Date of beginning of pupal stage	Length of pupal stage (days	Date of emergence of adult	Time from egg to adult (days)
July 17	12	July 29	20	August 18	32
July 17	11	July 28	14	August 11	25
July 18	12	July 30	11	August 10	23
July 25	8	August 2	10	August 12	17
July 25	10	August 4	12	August 16	22
July 26	9	August 4	12	August 16	21
July 26	9	August 4	16	August 20	25
July 26	12	August 6	15	August 21	27
Average	10.4		13.7		24

In June, 1919, the average larval period in the case of twenty-one first-brood maggots bred in the laboratory at Perry, was 9.4 days, with a range from 7 to 12 days. Specimens bred in the field cages required about two days more.

Habits of the larva

The larvae of *Hylemyia cilicrura* are instinctively internal feeders. When they hatch, the small larvae crawl thru the crevices of the soil in search of food. In this search they show a preference for material that is beginning to rot, and they are always most numerous in decaying beans. Seventeen maggots were once found in a slightly decomposed bean, and seven to ten is not an uncommon range. They may be found in sound

beans also, tho a sound seed rarely contains more than two or three. Beans that are entirely decomposed have no attraction for the insect.

In order to test the ability of a maggot to find its bean host, ten newly hatched larvae were placed on top of the soil in large vials, in July, 1917, and an unsoaked bean seed was placed at the bottom of each vial. Eight of the ten maggots found the bean and were reared to adults.

The pupa

Time spent in puparium

In the summer of 1917, the length of the pupal stage of eight specimens was found to be 13.7 days, as shown in table 2. The average length of the pupal stage of seventeen additional specimens, carried thru in the outdoor cage in July, was 12.8 days, the time varying from 10 to 14 days. In June, 1919, the average time required for nineteen pupae was 10.2 days, with a range from 8 to 14 days. The time required in a field cage, from the hatching of the egg until the emergence of the adult fly, was found to be 22.7 days for forty-five specimens, with a range from 16 to 27 days. Allowing 10 days for the larval stage, this would make the average pupal period 12.7 days. Cages have been examined for puparia tending to show a lengthened pupal period, but cases of retardation, such as those noted by Schoene for the closely related cabbage maggot (*Hylemya* [*Phorbia*] *brassicae*), have not been observed. In 1918, however, the rainfall at Perry during July and August was far below normal (table 6, page 971), and in the fall of that year only one fly of a possible third brood was seen. In both 1917 and 1919, third-brood flies were numerous. The absence of a third brood in 1918 might have been due to a lengthening of the pupal period of the second brood caused by the high temperature and low rainfall.

Place of pupation

Puparia of *Hylemyia cilicrura* are usually found near the surface of the ground, a short distance from the place of larval feeding. They are occasionally found as deep as six inches below the surface, but ordinarily not more than three inches below. In bean fields they are often seen within a few inches from the plant food of the larva.

The adult

Emergence

The emergence of what are believed to have been second-brood flies reached its height at Perry, New York, on July 13 and 14, 1917. The flies continued to appear in the rearing cages until about August 1. Flies reared from eggs deposited, no doubt, by this brood and hatching about July 25 and 26, produced, late in August and September, what was possibly a third brood. It is believed that an entire brood of flies was

missed in that year, owing to the delay in opening the laboratory. In that year the spring was very late and the rainfall was heavy thruout June and July.

In 1918 a few females with well-developed eggs were found on May 9. It is not definitely known whether these flies hibernated as adults or were very early specimens of a main brood which came later. Judging from the number of flies taken in the field, the maximum emergence of first-brood flies occurred between May 23 and 26. Second-brood flies appeared in the cages from June 26 to July 5. After July 23 only one fly was found. This was a male, taken on August 26. In that year there were apparently only two broods. The adults came out early in the spring, but, as a result of the hot, dry weather at Perry in late July either the flies died or the development of the stages of the following brood was retarded.

In 1919 a few flies were found after May 15, but it was not until June 2 that they were at all abundant. They could still be found easily on June 9, and occasionally until June 17. Most of the females deposited their eggs during the first week of June. Second-brood flies appeared in the cages from June 18 to July 3, with the maximum emergence about June 25. The hot weather of mid-July must have proved fatal to most of the flies, for they disappeared entirely and no more were seen until September 9. Then, for a few days, flies of the third brood were taken. In 1919 there were apparently three broods, or at any rate two and a partial third. The data leading to this conclusion are given in table 3:

TABLE 3. SUMMARY OF RECORDS TENDING TO SHOW THE NUMBER OF BROODS IN 1919

Date		Observations
May	15	3 ♂, 6 ♀, taken by sweeping, 2 ♀ containing well-developed eggs
	20	A few flies taken in an old wheat field
	27	Flies still scarce
	29	2 ♂, 3 ♀, taken, eggs small; few flies seen, weather cold
June	2	Flies plentiful; eggs in females ranging from partly developed to mature
	4	Eggs found on decaying material in cages, females in field containing a few mature eggs or no eggs
	9	Fewer flies; abdomens empty
		Small maggots found in beans planted June 2
	11	3 ♀ taken containing no eggs; abdomens collapsed
	19	First of second-brood flies emerged in cages
	20	13 second-brood ♀ from field examined, eggs undeveloped
	25	Many second-brood flies coming out
July	3	A few second-brood flies still coming out
	15	Weather hot, few flies
	26	No flies seen; flies in cages dead, probably owing to hot weather
Sept	13	1 ♂, 3 ♀, taken on ground plowed for wheat, eggs immature
	15	1 ♂ taken

In 1920 the first flies were found on May 7, and during periods of warm weather they continued to emerge in numbers until the first of June. Most of the eggs of this brood were deposited between May 25 and June 5. Weather conditions in July of that year were more favorable than in 1919, and flies lived in the cages until the first of August.

Dates of emergence vary greatly at different altitudes. Flies have been found in abundance, a week or more before the Perry emergence, at places ten miles from Perry where the elevation is much less. The bean laboratory was located on what is said to be one of the highest points between Lake Erie and the Genesee River, its elevation being 1400 feet. Data obtained at Perry, therefore, while holding true for much of the western New York bean-growing section, are probably later than for most parts of the State. The opening of spring at Perry is at least a week later than it is at Ithaca.

The time of emergence of *Hylemya cilicrura* is dependent largely on temperature. If there are several warm days early in May, some flies will appear. If such a warm period is followed by colder weather, additional flies may not be found for a week or two, or until the temperature has again moderated.

Length of life

Adults of *Hylemya cilicrura* have lived in cages for from 2 to 14 days. In 1920 nine flies under observation lived for an average of 26 days. Without food, life is short, but in cool weather the flies will live for many days in moist cages if they are supplied with sweetened water. The time in this period when eggs are deposited is not well known; but from the fact that adults with immature ovaries are normally found for many days before mature specimens appear, it is probably toward the end of the adult life. Many flies were taken by sweeping in the field on May 20, 1920, at which time most of the females dissected contained immature eggs. Flies taken at this time were placed in cages, and deposited eggs between June 1 and June 6. Apparently, then, the length of the preoviposition period is about two weeks.

Habits

The author's inability to obtain eggs from flies reared in captivity has already been mentioned. Molasses, sugar water, and decaying material were placed in cages, but all failed to supply suitable conditions. A large cage, six feet square, in which beans, cabbage, and mustard were growing and which contained decaying material also, failed to give any better results. Flies were attracted in large numbers by sugar water and molasses. In the field many flies were found in bait pans containing a mixture of molasses, water, and sodium arsenite.

In the spring the flies are attracted to moist, newly plowed ground. They crawl deep into the crevices of the soil, stopping occasionally to lap

up a drop of moisture as they find it. When the flies are moving about in this manner, the wings are overlapped on the back and are thus out of the way. Twelve flies have been counted in three feet of furrow, and forty-two were seen in a square yard. A count of the flies taken on new soil on May 27, 1918, showed fourteen mature females and one male. At this period or a little later, many flies may be taken by sweeping along the edges of fields and roadways. On June 18, 1918, many were caught in the tall grass at the edge of a field, a count showing about four males to every female. On July 8 there were forty-one males in a lot of forty-five flies taken by a roadside. It is apparent, then, that while the females are searching for places suitable for oviposition, the males may be found sunning themselves in grassy and weedy places. On sunny days, adults have been seen resting on mustard; and in the evening they are found on onion tops, kale, potato vines, daisy, and ragweed, and more rarely on other plants. Flies have also been observed hovering about a dead earthworm lying on the surface of the ground.

On warm days, or during the hotter part of the day, the flies are very active, crawling restlessly near the top of breeding cages; but in cold weather they move slowly over the dirt on the floor of the cage, or remain quiet in the cracks of the soil.

It was observed in the spring of 1919 that flies might be taken in the grass along roadsides, and in wheat and oat fields, before they made their appearance around plowed ground. It would seem, then, that as the egg-laying period approaches, flies have a tendency to come into the open and seek loose, moist soil. This is especially true if such soil contains, as an additional attraction, the decomposing roots of clover or quack grass.

HIBERNATION

The writer has little data on the hibernation of *Hylemyia cilicrura*. Cages have been placed in fields and meadows early in the spring, but no flies have emerged in them. Early in May a few flies with ovaries partly mature have been found. It is probable that these were early specimens of the subsequent first brood, which had wintered in puparia; but they may have been flies that had emerged late in the previous summer and had hibernated as adults. It has not been possible to keep flies that are taken in late summer, alive in cages thru the winter. The writer believes that the insects more commonly pass the winter hibernating as second-generation pupae, and emerge as flies from May 15 to June 1 of the next year. Such flies, taken in late May, had only partially developed ovaries and were fresh-looking specimens. In support of this pupal-hibernation theory, N. F. Howard[1] found *cilicrura* hibernating in the pupal stage in onions in Wisconsin, and Dickerson (1910) showed that from pupae of *cilicrura* placed in cages in November, flies would emerge early in May of the next year.

[1] Noted in a general discussion reported in the [illegible] vol. 9, p. 133, 1916.

SEASONAL HISTORY

Adult flies of the first brood are found in the fields from early in May until the middle of June, and deposit their eggs on decaying material or on moist soil about bean-planting time, during the last of May or early in June. The maggots work in beans, corn, potatoes, or rotting vegetation, and emerge as second-brood flies in July. These flies soon disappear in normal hot, dry summers, but apparently they deposit eggs about decaying vegetable matter before they die. A few third-brood flies may appear in August and September, some of which may hibernate; but most of the flies taken in May of the next year are believed to come from the midsummer brood of pupae which overwinter.

CONTROL

Control measures for *Hylemya cilicrura* may be classed either as artificial, such as seed treatment and the use of baits, or as cultural. The cultural methods involve studies of influential factors in the environment of the insect, and of practices used in growing the crop which may affect the extent of infestation by the maggots. The artificial methods are recorded first.

Artificial methods of control

The studies in artificial control that have been directed against *Hylemya cilicrura* in the past have been concerned mainly with seed treatments and with the application to the soil of such materials as would either kill the maggots or act as repellents for the adult flies and thus prevent the deposition of eggs. Lintner (1882a) suggests soaking the seed in gas tar or copperas to keep the maggots away, and Lugger (1896) says these materials work well on a small scale. Headlee (1913) tried solutions of corrosive sublimate, sulfocide, and potassium cyanide, in an effort to kill the maggots and prevent oviposition by the flies, but his results were unsatisfactory. Later (1918) he tells of trying strips of tar, and also of the application of sand treated with carbolic acid to the surface of the soil just after beans were planted. As a result of this treatment, a few more plants came up in the treated plots than in the checks. Still later (1920), Headlee found that a repellent effect on the maggots resulted from treating lima beans with coal tar and dusting them with ashes, lime, or tobacco dust. Chittenden (1909) suggests that carbolic acid might act as a repellent to the adult flies, and both he and Bruner (1910) advise the application of kainit, nitrate of soda, or sulfate or chloride of potash to the soil as a top dressing. In addition to discouraging oviposition, this practice is said to have the added advantage of stimulating plant growth.

While seed treatment and the application of insecticides to the soil may be of value when used in a small way, these practices are of doubtful importance as control measures on a field scale. An infestation of the

TABLE I.—EXPERIMENTS CONDUCTED AT PERRY, NEW YORK, IN 1917 ON SEED AND SOIL TREATMENT FOR THE SEED CORN MAGGOT

Experiment	Material	Manner of application	Number of seeds per lot	Date planted	Date examined	Number of seeds germinated	Number of stricken hills	Remarks
A_1	Hellebore	Drilled in	100	July 12	July 19	78	0	
A_1	Hellebore	Drilled in	50	16	23	20	0	
A_2	Hellebore	On seed	100	16	16	26	2	Hellebore mixed with cottonseed oil
B_1	Iron sulfate	On seed	50	12	19	28	3	2 pounds in 1 gallon of water
B_1	Iron sulfate	On seed	100	16	23	2	1	Flour added as sticker, germination hindered
B_2	Iron sulfate	On seed	50	16	23	5	0	Poured on seed in row
C_1	Borax	On seed	100	12	19	0	0	No germination, radicle injured
D_1	Carbolic emulsion	On seed	50	16	23	22	0	No injury, growth slow
E_1	Kerosene emulsion	On seed	50	16	23	0	0	Seeds rotted by drench
F_1	Sulfocide 1-1	On seed	100	12	19	12	0	Cotyledons decayed
F_2	Sulfocide 1-1	On seed	50	12	19	43	0	Good stand
F_3	Sulfocide 1-1	In row	50	12	19	45	0	Good stand
F	Sulfocide	On seed	100	16	23	22	0	Concentrated material injury resulted
G_1	Lime-sulfur 1-1	On seed	100	12	19	50	1	
G_2	Lime-sulfur 1-3	On seed	50	12	19	35	0	
G_3	Lime-sulfur	In row	50	12	19	0	0	Concentrated material, beans injured
G	Lime-sulfur	On seed	50	16	23	37	2	Concentrated material, beans rotted
H	Dry bordeaux	In row	50	12	19	0	0	Discolored seed coat, germination delayed
H_1	Dry bordeaux	On seed	50	12	19	37	1	Good stand
H_1	Dry bordeaux	On seed	100	16	23	78	1	Good stand
H_2	Dry bordeaux	In row	50	16	23	45	1	Good stand
H_3	Dry bordeaux	On soil	50	16	23	40	1	Good stand
I	Creosote	On seed	100	12	19	0	0	Beans rotted
J	Quassia solution	On seed	100	16	23	30	3	Normal spray solution, hop-tobis strength
J	Quassia solution	In trench	50	16	23	17	2	
K_1	Black leaf-40 1-1000	On seed	100	12	23	0	0	Seed decayed
K	Black leaf-40 1-1000	On soil	50	16	23	12	2	Slow growth
L	Sulfur	In trench	100	16	23	28	2	
M	Tobacco dust No. 1	On seed	50	16	23	30	1	Slow growth
M	Tobacco dust No. 2	On seed	50	16	23	1	0	Slow growth
R	Scalecide 1-15	On seed	100	16	23	25	2	
R	Scalecide 1-15	On soil	50	16	23	20	1	
	Check		100	12	19		1	
	Check		100	12	19		2	
	Check		50	12	19		1	
	Check		100	12	19		3	
	Check		100	16	23		1	
	Check		100	16	23		2	
	Check		100	16	23		1	
	Check		100	16	23		2	

seed-corn maggot cannot easily be predicted; its first indication to the grower is usually the discovery of the maggots in beans that have failed to germinate. Since this is true, an efficient repellent or seed treatment would have to be used every wet year, which would make the cost for material and labor very high. Furthermore, it is difficult to find a material which does not injure the seed and yet has a killing or repellent effect on the insect. Maggots usually enter the bean between the cotyledons, and therefore, after the seed coat, which bears the treatment, is broken or cast off by the swelling of the seed, the tender plumule is again left unprotected.

The writer has tried various materials as control measures, on a small scale, in the hope of finding something suitable for larger tests. The results of these experiments are recorded in table 4.

In the experiments reported in table 4, the materials were placed either on the seed coat, on top of the soil, or in the row with the planted seed. These experiments were located in fields where bad infestations of maggots had just been found and where the flies were very numerous. Infestations were not large, however, as the plantings came between broods. Dry bordeaux mixture seemed the most promising of the materials tested, but on the whole the results of experiments in 1917 were not encouraging.

In 1920, seed- and soil-treatment experiments were again conducted. A part of the experimental field which had not been under cultivation for several years, and which was covered with quack grass, was plowed, and the experiments were started here on June 4. At that time many females of *H. cilicrura* were mature and had been depositing eggs for several days. Beans were planted, following a rain of 0.25 inch, on June 3. It was noted that the flies had been more numerous on this part of the field than on the other parts which had been previously under cultivation, showing the attraction of the species to turned-under quack grass as a place for oviposition. Snakeheads, the evidence of maggot attack, were much more abundant here than in the main part of the field when counts were made on June 22. The results of the experiments of 1920 are given in table 5.

None of the materials tested in 1920 gave promise of success in practical use. While in a few cases the number of injured plants was reduced, in no case did the seedlings entirely escape harm. Taking into consideration the difficulty of predicting infestations of the seed-corn maggot, it seems to be unwise to rely on control measures of this type in New York.

The bait of sodium arsenite, water, and molasses, which was tried against the onion maggot by Sanders,[5] was tested against *H. cilicrura*. On June 21, 1917, the material was sprinkled on the soil with a whisk broom, and pie tins containing it were placed in a row across the field. Flies were very numerous in this field and the second planting of beans had just been made, the first seeding having been destroyed. On the morning of June 22, twenty-nine flies were found in the pans, together with many beneficial

[5] As stated in a general discussion reported in the *Journal of Economic Entomology*, vol. 8, [illegible] 1915.

TABLE 5. EXPERIMENTS IN 1920 ON CONTROL MEASURES FOR THE SEED-CORN MAGGOT

Experiment	Material	Manner of application	Number of seeds planted	Number of seeds germinated	Number of Stockheads	Number Stockheads injured	Per cent of beans injured: Inoculation to those germinated	Per cent of beans injured: Inoculation to those planted	Remarks
Check			50	46	45	20	43	40	
A	Sulfur	In hole	100	92	84	38	41	38	
B	Sulfate of potash	In hole	100	92	84	38	41	38	
C	Calcium cyanamid	In hole	100	92	85	40	43	40	Burning resulted
D	Nitrate of soda	In hole	100	93	85	40	43	40	Burning resulted
Check			50	44	42	11	25	22	
E	Acid phosphate	In hole	100	95	87	23	24	23	
F	Ehasto	In hole	100	94	87	22	23	22	Injury resulted
G	Ammonium nitrate	In hole	100	93	86	25	27	25	
H	Ground limestone	In hole	100	94	87	23	24	23	Growth slow
I	Nitrate of potash	In hole	100	95	87	23	24	23	
Check			50	49	46	11	22	22	
J	Dried blood	In hole	100	94	87	23	24	23	
K	Cat-tobe	In hole	100	96	87	23	24	23	
L	Dry fish-scrap	In hole	50	48	43	11	23	22	
Check			100	94	87	23	24	23	
M	Tobacco dust	In hole	100	96	88	24	25	24	Growth delayed
N	Kerosene and lime	On soil	100	94	87	23	24	23	
O	Carbolic emulsion 1–20	In hole	100	96	88	24	25	24	Injury resulted
P	Tarred sand	On soil	100	96	88	24	25	24	
Q	Nicotine sulfate 2–50	On seed	100	96	88	24	25	24	
R	Bordeaux paste 1–50	On seed	100	95	87	23	24	23	
S	Lime-sulfur 1–20	On seed	100	96	88	24	25	24	
Check			100	96	88	24	25	24	
T	Carbolic and lime	In hole	100	96	88	0	0	0	Injury resulted
U	Creosote and lime	In hole	100	96	88	0	0	0	Injury resulted

carabid beetles. No dead flies were seen in the field outside of the pans, and later, when the beans came up, there was no reduction in the number of snakeheads near the pans. Pans were placed in other fields, and, tho many flies were captured, no great benefit was noticeable when the beans were examined two weeks later.

Before planting was done in this field, which was very wet, the seed was drenched with kerosene. Eight days after planting, the counts showed 49 maggot-infested seeds out of 110 that were examined. When the seed was treated overnight with carbon disulfid, 17 out of 57 beans contained larvae of *H. cilicrura*. A check had 28 infested seeds in 50. Altho neither material injured the germination of the seed, there was little if any repellent effect produced.

Beans were treated also with arsenate of lead in the form of a strong paste. This was allowed to dry and the seed was then placed in the ground with a bean planter. The poison so injured the seed that only about 15 per cent germinated. A check showed an 85-per-cent stand.

Neither seed treatment nor other artificial control measures have given promise of success. No satisfactory material has been found, and nothing that looks promising for tests on a large scale has been discovered.

Natural and cultural methods of control

There are many factors bearing on the presence or the absence of *Hylemyia cilicrura* in a field. Some of these are discussed in the following pages, and practices which are in the nature of preventives are pointed out.

Moisture and temperature as factors in the life of the seed-corn maggot

Hylemyia cilicrura has been found to be a serious pest in New York when the early summer is rainy. This increased injury in moist seasons is apparently due to the tendency of the cultivated hosts to decay in the wet soil, thus becoming attractive to the flies as a place for oviposition. It seems probable, also, that maggots already in the soil feeding on other decaying vegetation, are attracted to the beans when they begin to decay.

In June of 1916 and also of 1917, the rainfall far exceeded the normal. In 1917 the June rainfall (6.4 inches) was more than twice the monthly average for the previous twenty years, and the damage from *H. cilicrura* was severe in all the bean-growing sections of the State. July of that year was rainy also, and thruout that month flies could be taken easily altho normally they are scarce at that season. The years 1918, 1919, and 1920 were nearly normal, and the loss was slight. In table 6 are given data from the United States Weather Bureau at Rochester, New York.

In periods of drought such as prevailed at Perry during July and August of 1918, flies are difficult to find. By July 22, 1918, only six flies of many hundreds were still alive in the cages, and on the following day not a fly

could be found in the field. On August 26 one male of *H. cilicrura* was taken, and this was the only fly seen in 1918 after July 22. The conditions at Perry in that year were abnormal, for this region suffered much more for want of rain than did the surrounding places. The reduction in the number of flies appearing at Perry in 1919 is possibly due to this prolonged dry period.

TABLE 6. TEMPERATURE AND MOISTURE RECORDS OF THE UNITED STATES WEATHER BUREAU AT ROCHESTER, NEW YORK, DURING THE SUMMERS OF 1917 TO 1920, INCLUSIVE

(Records of marked variations from the Rochester records found at Perry are given in boldfaced type)

Month	Mean temperature (Fahrenheit)					Rainfall (inches)				
	1917	1918	1919	1920	Normal	1917	1918	1919	1920	Normal
May	49 2	61 7	56 4	55 8	56 7	3 16	1 75	5 20	0 78 **2 01**	2 94
June	62 8	62 6	72 8	65 7	66 1	6 40	2 40	2 96	1 15	3 13
July	71 7	70 2	72 2	67 8	70 4	4 23	2 70 **1 03**	3 49 **1 21**	2 93	3 09
August	69 0	71 5	67 8	70 3	68 3	2 51	1 83 **1 34**	3 60 **5 70**	1 51	2 96

In July of 1919, the rainfall at Perry was again below normal, and the flies in the cages died rapidly after July 1. Between July 1 and July 20, the rainfall was only 0.67 inch, and the maximum temperatures for this period ranged from 65° to 96° F. After July 15 no flies were seen for two months and the specimens in cages all died. August of that year had nearly twice the normal rainfall.

The temperature early in the summer appears to have an influence on the abundance of *H. cilicrura*. In 1917 the mean temperature for May was 49.2°, which is several degrees below the average for the month and is the lowest recorded since 1871. The maggots and flies during that season were the most numerous in the history of the insect. June temperatures in 1917 also were lower than the normal, and had been each year since 1913.

H. cilicrura is an insect which in the past has been injurious for one year, or for a few successive years, and has then become of negligible importance for an indefinite period. This variation is undoubtedly connected to some extent with the moisture and temperature conditions of the early summer. Moderately low temperatures with an abundant rainfall in the spring appear to be favorable to the insect, while dry, warm weather during the summer is detrimental to its successful development. A succession of cold, wet years brings forth the insects in greatest numbers.

Relation of time of bean planting to time of oviposition

Eggs may be deposited by *Hylemyia cilicrura* near decaying vegetable matter in newly plowed or recently fitted soil before the beans are planted, while they are being planted, or even after planting. In rare instances a combination of these two possibilities may be found. When the eggs are deposited previous to planting, the maggots feed on decaying matter in the vicinity for a while, becoming nearly full-grown before they enter the bean seed; but when the eggs are deposited subsequent to planting, small larvae will be found in the beans within a few days after they are planted.

As examples of oviposition in the soil before the beans are planted, the following instances may be mentioned. In the experimental field at Perry, in 1919, one piece was plowed on May 14 and planted on May 28. When it was examined on June 5, many full-grown maggots were found. Allowing ten days for the larval period and two days for the egg stage, the eggs were probably deposited about May 24. A field that had been in alfalfa for several years was plowed for beans in May. Planting took place on June 6 and 7, and when the field was examined on June 12 the maggots present were ready to pupate. These maggots were hatched from eggs deposited probably about June 1. Maggots of about the same size were found in the old alfalfa roots.

As illustrations of egg-laying either at the time of planting or subsequent to it, the following examples are given. In 1919 a field of beans was planted on June 2. When it was examined on June 9, maggots a few days old were found. Flies were very common in the field on June 2 when the seed was drilled in. Beans were planted in a test plot on the experimental field on June 5. On June 10, when these were examined, some contained newly hatched maggots. In a field in Niagara County beans were planted on June 9. Small maggots were found feeding on the plumule leaves on June 14.

In the rainy year of 1917, when *H. cilicrura* could be found everywhere, fields were inspected late in June. Small and large maggots were found in the beans, pupae were in the soil, and flies with eggs in all stages of development were hovering over the ground. It is only late in the spring of very wet years that all stages can thus be found simultaneously. In more normal years the flies seem to appear in roughly defined broods, and the heavy oviposition of each brood does not extend over a period of more than a week.

From the foregoing data it is evident that a grower cannot be sure that maggots are not already working on other matter in the soil at the time when he plants his beans. Moreover, if mature flies are numerous at planting time, his beans may be infested with maggots from eggs deposited at that time.

In 1919 an attempt was made to connect the time of fly emergence and the time of oviposition with some of the more obvious occurrences in

nature. In that year, and also in 1920, the first flies were taken in small numbers early in May, about the time when cherries were in bloom. Mature flies were out in numbers near plowed ground on June 2, 1919, at which time the last of the petals had fallen from late apple trees at Perry. Flies with fully developed eggs had not been found in quantities on plowed ground before this, altho a few females with immature eggs had been collected in winter-wheat and oat fields. Many eggs were deposited in cages about June 4. Dissected females showed that some eggs were mature on June 2 and many on June 4. It is evident, therefore, that under Perry conditions in 1919, beans planted between June 2 and 12, or within ten days after the last of the petals had fallen from the late apple trees, were open to maggot attack. Serious infestations of maggots were very few in 1919, but in two bean fields which did show *cilicrura* injury the seed was planted on June 5 and June 6, respectively.

On May 28, 1920, when the petals had partly fallen from the late apple trees, flies nearly mature were found in numbers on moist, newly turned ground, especially where the field had previously been in sod. After May 7, when the first specimens of the year were taken, adult females were captured almost daily and their abdomens examined for eggs. Between May 7 and May 28, a few flies with ripe eggs were occasionally found, showing that eggs were doubtless deposited in small numbers during that period. A cornfield planted on May 22 and examined on May 29 showed typical *cilicrura* injury in a few seeds. However, this examination of females taken thruout May showed that most of the first brood of flies were not mature before May 28. At that time there were many more females than males present on plowed ground. Many eggs were deposited between May 28 and June 7 by flies in the cages. Most of these eggs were deposited after June 4, when the nights as well as the days were warm and the flies showed unusual activity.

Many fields in which beans were just appearing above ground were examined on June 7, 1920, and only six infested plants were found. Good weather had made it possible to plant some of these beans by May 21, and all were in before June 4. Therefore, in these fields, the seed was in the ground before most of the flies were mature, with the result that there were but few maggots in the soil.

Beans planted in the experimental field on June 4, 1920, were heavily infested, and potatoes and corn planted in neighboring fields about the same time contained many maggots. This infestation is probably due to the fact that the seed was put into the ground at the time when the flies were mature and eggs were being deposited. Beans planted in the middle of June were uninjured. From these data it would seem that beans planted just after the last apple blossoms have fallen, which under the conditions at Perry in 1919 and 1920 was from May 28 to June 7, stand a greater chance of being infested by the maggots of *H. cilicrura* than do those planted

before or after these dates. Since the larvae already in the soil may attack the newly planted seed, it is wise to delay planting for a few days after all the eggs have been deposited. This would extend the time for probable infestation in 1919 and 1920 from May 28 to about June 15. Unfortunately, it is not always possible to choose the time of planting as suggested above. Weather conditions may prevent planting in May, before the flies are mature, and if beans are put in too late in June they may not ripen before they are killed by frost. Seasons vary so much from year to year that no absolute rule can be given; but, if weather permits, it is best to plant before the oviposition period of the flies, when the last of the petals have fallen from late apple trees.

Relation of kind and condition of soil to maggot infestation

Abundant moisture provides favorable conditions for the development of *Hylemya cilicrura*, as is shown on page 970. Beans on heavy soil, which holds moisture, grow more slowly, decay, and furnish conditions attractive to the flies for oviposition. In 1917 one side of a bean field near Perry was badly infested, while the remainder, which was planted on the same day, was free from injury. An examination of the soil in the infested part showed it to be heavy and sticky, while the unattacked beans were growing in lighter soil of a sandy constituency, which was relatively dry. The division between the two types of soil was very marked, and the good and the poor beans followed this line closely. Well-drained fields are not attacked as often as are those where the drainage is poor. Low and wet spots, where water may collect in otherwise good fields, often yield poor beans. This is in part the result of maggot work, but it may often be due to the decay caused by the excess of moisture in the soil.

Warm, dry soil that is well fitted furnishes ideal conditions for the growth of beans. In soil of this kind they will germinate quickly, and when once above ground there is little chance of serious injury from maggots. In wet seasons it is best to delay planting until the soil can be well fitted. A field should be dragged and rolled, and the top layer of earth allowed to dry out and become warmed by the sun.

Influence of preceding crop and time of fitting a field, on maggot attack

Heavy infestations of *Hylemya cilicrura* have been found on land that had previously been in potatoes, corn, tomatoes, wheat, oats, and beans, as well as in clover and alfalfa sod. Many infestations have followed sod, since the upturned roots of decaying clover and alfalfa furnish good breeding conditions for maggots, and since clover forms a part of a regular rotation of beans, wheat, and clover which is practiced in western New York. Just as serious outbreaks have been found, however, where the preceding crop was beans, especially if the field had an abundance of quack grass and weeds. In the writer's garden there was a patch of quack grass. This was turned under, and beans and peas planted on

this spot were infested with maggots, tho in other parts of the garden there was no injury.

Whelan (1916) has found maggots in fresh manure, and he says:

> Furthermore, it appears that while beans were apt to suffer when planted on freshly turned clover sod, especially if recently fertilized with undecomposed manure, they stood a much better chance of escape if the field was prepared early in the season and the maggots given a chance to develop and disappear before the beans were planted.

Tho the writer has been unable to find evidence of flies breeding in manure, he has found many maggot-infested fields which had been covered with manure just before plowing. It must be said, however, that serious outbreaks have been found where manure was not used.

If a field is fitted early and is allowed to dry out before the mature flies seek places to oviposit, it appears to be less attractive for oviposition than newly turned soil. In 1920 the laboratory field was plowed at a time when flies with well-developed eggs were numerous, and many bean seedlings were infested. Fields near by that were plowed earlier and allowed to stand were free from maggots.

Relation of depth of planting to injury by maggots

Beans planted deep in the ground take longer to reach the surface and are thus exposed for a longer period of time to maggot attack. It has been observed many times that beans planted deep in wet ground suffer more from *Hylemyia cilicrura* than those that are planted less deep. For example, in 1917 it was often noticed that the headlands yielded better beans than the remainder of a field. This is attributed to the more shallow planting, for the soil was not so loose at the edges of the field and therefore the drill did not sink so deep.

In 1917 a field under observation had nearly every bean attacked by maggots. The seed had been planted in wet soil at a depth of from three to five inches. After this first planting was destroyed by maggots, the field was reseeded at once, and the beans were dropped as near the surface of the ground as possible. Some of the seed was even left on top of the soil, and a boy with a hoe followed the machine to cover the beans left exposed. A 95-per-cent stand resulted.

In another case a grower started to make a very shallow planting of beans. When he had gone part of the way across the field, he decided that he was not getting the seed in deep enough, and so he planted the remainder of the seed much deeper. At harvest time the beans planted first, the shallow-planted ones, were the only ones worth harvesting. If the beans are planted too deep, many will decay because of the excessive moisture, and the maggots will destroy a large proportion of the remainder.

Experiments were conducted in 1917 to test the effect of the depth of planting on the time required for the beans to break thru the soil. Beans were planted on good, tho very wet, soil on July 12. When the field was

examined on July 19, the beans that were planted about one inch deep were nearly all up, those planted three inches deep were about half thru the soil, and none of those planted five inches deep were yet above ground. In another wet field 100 seeds were planted at depths of one, three, and five inches, on July 16. On July 23 there were, in the one-inch planting, 57 plants, of which 4 were snakeheads; in the three-inch planting there were 35 plants, of which 5 were snakeheads; and none of the beans planted five inches deep had appeared above ground. In the laboratory field, under rather warm, dry conditions in July, 1918, it was found that beans planted three inches deep came up nearly as quickly as those planted more shallow.

Summary of preventive measures

The results of experiments on artificial control measures, such as coating the seed before planting and treating the soil with materials of a repellent nature, afford small hope for their future successful development. As a result of a study of some of the factors governing infestations, the possible preventive measures that have been discussed in the foregoing pages are summarized in the following paragraphs.

The seed-corn maggot is more serious as a pest when the months of May and June are rainy, and the ground is cold and wet at bean-planting time, than under other conditions. The greatest injury results when several unfavorable years occur in succession. *Hylemya cilicrura* thrives when oviposition takes place under wet conditions, and therefore it is wise to plant when the soil is dry and the earth is warm. The soil should first be well fitted with a disk or a harrow, and then rolled, and finally, after a few warm days have dried out the top soil, the beans should be planted. If the field is fertilized in order to hasten the germination of the seed, there is a still better chance of getting a stand. However, fields fertilized with fresh manure just before plowing often show a heavy infestation of maggots, and so this condition should be guarded against in wet years.

As maggots developing from eggs deposited on newly tilled ground are often found in decaying matter in the soil, it is sometimes wise to fit a field early, before most of the flies are sexually mature. The ground will then be dried and less attractive to flies for oviposition by the time they come out. The presence of many flies of this species crawling over newly turned soil between plowing and planting time is a good indication that seed planted there will probably be infested. In 1918, 1919, and 1920, sexually mature flies were most numerous in the fields at Perry from May 25 to June 10. In 1919 the greatest number were present about June 4, and in 1920 about June 2. If the weather permits, it is better to plant ahead of this brood. If this is impossible, planting should be delayed until the flies are less common.

It is extremely important that beans should not be planted too deep in wet soil. If they are, some of the seed will rot and the maggots will destroy

most of the remainder. Not only is the soil three or four inches below the surface much colder and more moist than the top inch, but also the deeply planted seed germinates more slowly in wet years. It is wise to force seed to germinate and grow as rapidly as possible, since it will have escaped serious injury when it is once above ground. If in shallow planting some of the beans are left on top of the ground, they may easily be covered with a hoe. A bean planter or a corn planter usually will give better service than a drill in wet years, for either is lighter and will not sink so deep in wet places. If a drill is used, it should be adjusted to make a shallow planting. A grower who plants his seed deep in wet soil at a time when the sexually mature flies are numerous, is sure to have a heavy infestation of maggots on his beans.

THE IMPORTED FIELD GRAY SLUG

(*Agriolimax agrestis* L.)

ORIGIN

The field gray slug, or garden slug (*Agriolimax agrestis*, Plate LXIX, 6), is an imported species which, with two other foreign forms (*Limax maximus* L. and *L. flavus* L.), does more damage and attracts more attention than all of the other twenty-nine species of slugs reported from the United States (White, 1918). *A. agrestis* is an old resident of Europe, having been listed in England as early as 1674. Taylor (1907) reports it in the fossil rocks of the Pliocene and Pleistocene periods from many places in the British Isles, as well as from Germany and France. It apparently came to this continent from Europe early in the eighteenth century.

HISTORY AND DISTRIBUTION

Theobald (1905) states that *Agriolimax agrestis* is found in nearly every garden in England, and also on the continent of Europe and in Siberia, Madeira, and Algeria. Taylor (1907) states that it occurs also in Turkestan, China, Japan, Asia Minor, Morocco, Cape Colony, Zanzibar, Australia, and New Zealand, as well as in Brazil, Jamaica, and parts of Canada, on this continent.

In the United States it was first reported near the seaports of Boston, New York, and Philadelphia. De Kay (1843) states that Binney knew it before 1843, tho Binney (1851) still had trouble in separating *A. agrestis* from the native species *A. campestris*, which it very much resembles. Since 1851 *A. agrestis* has spread gradually westward, and it is now found locally in many States. Its presence is reported in the literature of Maine, Massachusetts, New York, Pennsylvania, Michigan, New Jersey, Illinois, Wisconsin, Ohio, Colorado, Washington, and California, but it is probably present also in many other parts of the country. Slingerland discovered the slug at work on the college farm at Ithaca in 1891. Baker

(1902) did not find it around Chicago in 1902, tho it had been reported from Michigan in 1899. Cockerell[6] found *agrestis* in Colorado in 1890, and he states that it was brought there from New Jersey. He reports it also in Oregon in 1891 and in California in 1892.

In western New York the localities infested by *A. agrestis* are increasing, and in wet seasons many beans, as well as other field and garden crops, are injured. The insect is apparently not a pest in all sections of the bean-growing counties, but appears to be limited to a few farms and gardens in each district. Some places seem to be entirely free from it. It is often abundant on small truck farms, and around the shrubbery and the gardens in city lots. It has, no doubt, been carried into its present habitats in the straw or moss packing of bulbs, shrubs, or nursery stock. Disseminated in this way, it seems to thrive, and it apparently prefers cultivated crops to woods and pasture land. As it becomes better established the species may be expected to spread from the present centers of infestation until it is of almost general distribution. The long, cold winters often experienced in New York, however, should tend to prevent the serious damage that it causes nearly every year where the climatic conditions are milder and more uniformly moist.

SYSTEMATIC POSITION

The field gray slug belongs to the phylum Mollusca and the class Gastropoda, which includes the slugs and the snails. *Agriolimax agrestis* is placed in the family Limacidae, the members of which have no external shell. This family, according to Pratt (1916), is represented in America by only six species. The large spotted slugs of the family are now placed in the genus Limax L., while smaller forms, such as *agrestis*, belong in Agriolimax Morch. Because of its varied coloration, this slug has been described under many specific names. Taylor (1907) gives a complete synonymy for the species, and lists ten varieties, with the localities from which each has been reported.

GENERAL DESCRIPTION OF THE SLUGS OF THE FAMILY LIMACIDAE

The field gray slug belongs to the same group of Mollusca as the snails, and differs from them but little except in the size and form of the shell. In slugs of the family Limacidae no shell is visible on the outside of the body, but there is a thin calcareous plate (Plate LXIX, 5) concealed in the mantle, the fleshy shield over the front part of the slug. The body is elongate-subcylindrical, and bears a more or less prominent dorsal keel. On the retractile head are two pairs of tentacles; the anterior pair are sheathing, while the upper, or posterior, pair bears the eyes. The eyes have the form of rounded knobs on filament-like stalks. When the slug is disturbed,

[6] As cited by Taylor (1907, 120).

the eyes may be withdrawn down the tentacle, and in young, transparent specimens they may be readily seen even after they have been retracted into the head. Slugs have the power of secreting from pores in the body, and especially from the anterior ventral surface of the foot, a slimy substance known as *mucus*. The shell-concealing mantle has, near its posterior lower border on the right side, a circular breathing pore which opens into a respiratory chamber beneath. This is lined with a richly vascular epithelium subserving the function of a respiratory organ. Just behind the right eye-stalk is the opening of the genital organs, thru which eggs are extruded. Slugs of this group are hermaphroditic, both male and female genital organs being present in a single individual.

ANCIENT SUPERSTITIONS CONCERNING SLUGS

Slugs have been known in Europe for many years, and the older writings in regard to them contain many interesting notes. They have been used as food in Europe, and it is said that as late as 1863 they were prescribed by French physicians, to be taken in the form of a sirup. A slug distillate was considered good for the complexion (Kingsley, 1885). A plaster of slugs with the heads removed, bound on the forehead, was believed to cure a headache, and slugs eaten alive in milk were thought to cure consumption (Rogers, 1908).

As slugs always appear after a rain, they were believed by English farmers in the eighteenth century to come from heaven in a rain cloud (Theobald, 1895). Since toads gather in infested fields to feed on the slugs, it used to happen that gardeners and farmers of a hundred years ago, finding that their plants had been destroyed during the night, would blame and kill the toads, while the real culprit was concealed in a safe retreat under ground (Ritzema Bos, 1890). Later, the value of toads as enemies of the slugs was appreciated and three francs a dozen was paid for them (Guénaux, 1904). Years ago the small shell of the slugs was regarded as an amulet, which, worn on a string around the neck, was believed to protect the wearer from harm. When the slugs suddenly appeared in large numbers in the gardens of European countries, it was customary to invoke the power of the Church against them, in the hope that they might be thus removed (Kingsley, 1885); and Taylor (1907) states that the Ritual of Paris, A. D. 1712, contains definite exorcisms for this purpose.

PECULIAR HABITS OF SLUGS

Some slugs are said to have a partiality for moist newspaper, dead fish, earthworms, dead clams, dead slugs, meal, flour, cream, butter, Pears' soap, sponge cake, and book bindings, as food (Cooke, 1895). They have been known to eat out the corks of wine bottles, to crawl into nearly empty beer bottles and bathe themselves in the contents, and even to attach their small mouths to the dripping faucets of containers of

alcoholic beverages. They will crawl into beehives and feed on the honey, apparently immune to the stings of their enraged hosts (Reh, 1913).

ECONOMIC IMPORTANCE

In wet years the field gray slug is one of the two most destructive animal pests of field beans in New York. During the rainy summers of 1916 and 1917, nearly all of the plants in some fields were attacked and many were entirely destroyed. Estimates of the losses on twenty-one farms in Orleans County in 1917 varied between 5 and 70 per cent. In 1918 the writer saw a bean field in Monroe County in which about one-third of a ten-acre field was so badly attacked that not a trace of a plant was left above ground.

In addition to its attacks on field beans, the slug often causes much injury to garden beans, lettuce, cabbage, peas, potatoes, radishes, and strawberries. As the species becomes better established in the farms and gardens in new localities thruout New York, it is probable that more widespread attacks may be expected on crops during wet seasons.

NATURE OF THE INJURY TO BEANS

Immature specimens of *Agriolimax agrestis* eat the tender tissue between the veins and the veinlets of the leaves, thus giving them a skeletonized

FIG. 91 INJURIES CAUSED BY AGRIOLIMAX AGRESTIS

A, A bean pod showing a hole made by the slug in feeding. B, Bean plants injured by [illegible] (Photographed in [illegible]). C, Bean plants that were injured by slugs soon after they [illegible] ground, photographed at harvest time. (Photo[illegible] above)

appearance. Older slugs, however, eat parts from the edges of the leaves, and frequently continue to feed until every leaf is devoured (fig. 91, B).

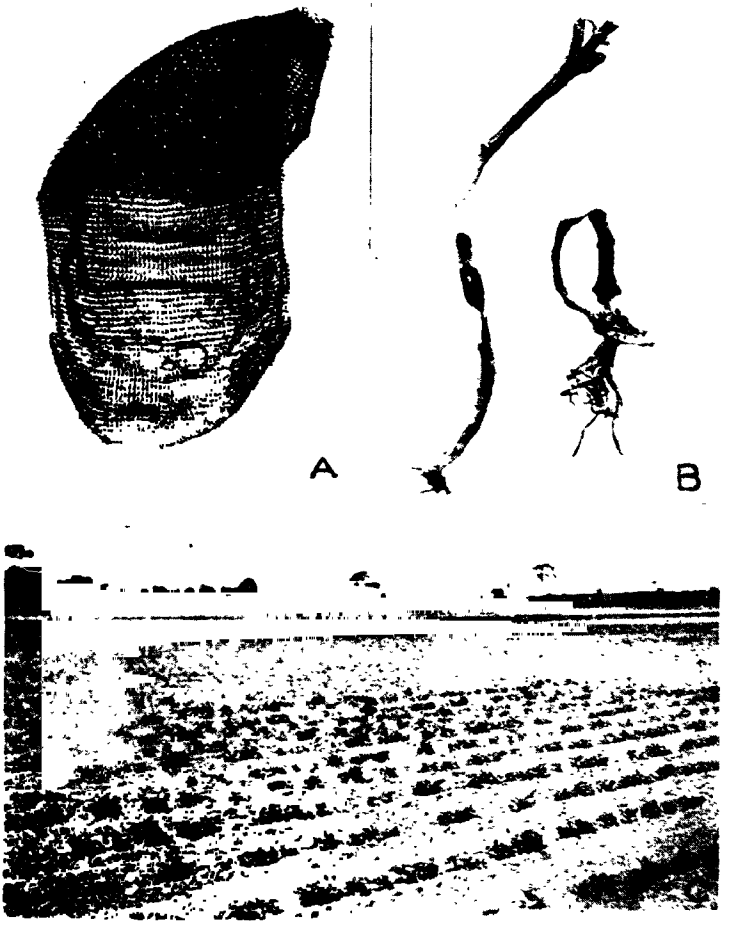

FIG. 92. RADULA OF AGRIOLIMAX AGRESTIS, AND RESULTS OF WORK OF SLUG

A, Radula, or lingual ribbon, of slug, made up of many hundred small, sharp teeth, × 25. B, Young bean plants showing result of feeding by the slug. C, A bean field in Monroe County, New York, in parts of which all the plants were destroyed by slugs; bare areas shown.

Sometimes the petiole and a few of the main veins are left, but oftener the entire plant above the surface of the ground is destroyed. During

the daytime and in dry weather the slugs feed beneath the ground, eating large parts of the stems of plants (Plate LXX, 2, and fig. 92, B). Such plants may be so severely injured that a wilting of the parts above ground results.

When a slug crawls up the stem of a young bean plant, it usually devours the budlike growing tip before it moves on to the leaves. Plants of this kind are always stunted and show an abnormal, useless growth of small leaves (fig. 91, C). Such plants commonly die, and even when they survive they fail to produce mature seeds.

If the slugs are numerous at the time of pod formation, it is not unusual for them to eat holes into the sides of the pods (fig. 91, A) and feed on the soft beans within. Often several holes of this kind are found in a single pod, and sometimes a slug after destroying one bean will move along inside the pod and feed in turn on all the remaining seeds.

INJURY TO PLANTS OTHER THAN BEANS

In its nocturnal feedings above ground, *Agriolimax agrestis* seeks the tender leaves of lettuce, corn, cabbage, and cauliflower. The injury which the slug does to these plants is similar to that which it produces on large bean leaves, and causes the plants to become unhealthy and unmarketable. When the weather is such that the slugs are active in late summer, they frequently eat large holes in the sides of ripe tomatoes and fall strawberries, in addition to eating the leaves.

The pest feeds underground on potatoes, and, together with the millepede *Julus caeruleocinctus* Wood, causes considerable damage in western New York by eating out large cavities in the tubers. Carrots, turnips, radishes, and beets suffer similar attacks on their fleshy roots.

HOSTS AND POSSIBLE FOOD SUPPLIES

Agriolimax agrestis has such a wide range of food plants that it is classed as almost omnivorous. Among the plants which it feeds upon are cabbage, potatoes, eggplant, lettuce, beans, lima beans, peas, corn, strawberries, gooseberries, cucumbers, melons, cauliflower, wheat, turnips, beets, carrots, radishes, celery, clover, oats, dahlia, dandelion, dock, chicory, tobacco, hops, and tomatoes. There are also many weed hosts on which this mollusk may be found, such as burdock, ragweed, lamb's-quarters, and mustard. It finds palatable several species of mushrooms also, and many ornamental shrubs and vines, and it finds abundant food in sod land and in lawns. Overgrown places in fence corners and along the edges of fields often harbor many of the slugs. Manure is acceptable to them as food, and their eggs, as well as young slugs, have been observed in large numbers where manure had been scattered in piles around a field. Cooke (1895) mentions as among the possible foods of *agrestis*, may-flies, beetles, and dead

slugs; Lovett and Black (1920) add sow bugs, earthworms, and aphids to this list; Taylor (1907) records a case in which *A. agrestis* killed and ate slugs of the species *A. campestris* when the two were placed in the same box; and Lebour (1914–15) finds that they eagerly devour the proglottides of Moniezia, a tapeworm of sheep. It would seem, therefore, that, while the slugs usually prefer a vegetable diet, under some conditions they relish animal food.

DESCRIPTION OF STAGES

The egg

The egg of *Agriolimax agrestis* (fig. 87, C, page 954) is elliptical or spherical in shape, and is translucent, jelly-like, bluish white, and iridescent. Under magnification the thin outer covering is found to be slightly roughened with regular raised and depressed areas. The eggs are found either singly or in masses, in the latter case being held together by a transparent secretion. On one end the small, projecting micropyle is visible, especially in newly deposited eggs. The eggs vary from 1.6 to 3 millimeters (1/16 to 1/8 inch) in length.

The young slug

A newly hatched specimen of *Agriolimax agrestis* is without definite form at first, but it soon assumes much the same appearance as its parent except that its tentacles are relatively larger and its body is transparent, permitting the black nerve cord running to the eye to be easily seen thru the body covering. Young slugs have a pinkish tint at first, but later turn to darker hues as they begin feeding.

The full-grown slug

The slug (Plate LXIX, 6, and fig. 87, D) is described by Taylor (1907:105) as follows:

> Animal limaciform, with large but flattened tubercles, of a somewhat uniform whitish or pale ochreous ground colour, but sometimes dull lavender or other tint, often mottled, speckled or reticulated with brown or black, and at times totally suffused with black, body somewhat compressed and keeled towards the tail; tentacles dark coloured; shield more than one-third the total length of the animal, rounded in front and behind, concentric striae not deep, with the nucleus on the right side and towards the rear, respiratory orifice with a broad usually unpigmented raised ring, which is cut anteriorly by the anal cleft; sole pale and longitudinally tripartite, the side areas sometimes darker, especially towards the tail; sole-fringe separated as usual from the body by a furrow, containing a row of elongate tubercles, upon which the body tubercles rest unconformably. Mucus plentiful and viscous, often clear when crawling, but becoming milky-white on irritation, due to innumerable particles of carbonate of lime.
>
> Length usually about 35 mill.

LIFE HISTORY AND HABITS

The egg

Under New York conditions, some of the eggs of *Agriolimax agrestis* are deposited in the fall, from August until December, and many of the mature slugs die soon afterward from the cold. If full-grown slugs live thru the winter, they may deposit eggs during May and June of the following spring. Slugs developing from these overwintering and spring eggs will mature and in turn deposit eggs in the fall of that year or in the following spring.

In the summer of 1917, which was very wet, eggs were deposited more or less continuously from May to December, being especially numerous in September and October. Theobald (1905) reports this to be the normal condition in England. Lovett and Black (1920) state that in Oregon egg-laying occurs at all seasons of the year, and that the greatest number of eggs are deposited in the spring and early summer.

In 1918, which was a drier and more nearly normal season for New York than the preceding years had been, eggs were deposited by the slugs in cages during May and June, and not again until September 23. In that year, as well as in 1919, most of the eggs were deposited late in October and during November. Moisture is a factor of great influence. A few of the eggs deposited in July and August of 1917 hatched that fall, but whether these young slugs survived the cold winter that followed is not known.

The dates of hatching for eggs deposited on May 4, 1918, by an overwintering slug were as follows: May 27, three; May 29, two; June 1, four, and June 2, five. The average length of the egg stage was 26.5 days. Eggs that had been deposited late in the previous fall hatched between May 10 and June 6, the length of the egg stage in this case being between six and seven months. Early in the summer all the slugs in the fields are about the same size, and it is therefore probable that the fact that some eggs are deposited in the spring and others in the fall has little influence on the hatching date.

During the winter of 1917–18, there was in the greenhouse, where the temperature ranged from 55° to 75° F., a wide variation in the length of the egg stage, which ranged from 26 to 57 days, the average for 180 eggs being 37.3 days. In a greenhouse which was kept at a constant temperature of 80° F., 24 eggs hatched in an average of 24.3 days. Theobald (1905) gives from three to four weeks as the normal egg stage in England.

The eggs of *A. agrestis* are tucked into crevices of the soil, not far below the surface of the ground, and are also hidden under rubbish and projecting stones, around the walls of buildings, and among the roots of grass. In bean fields that have been badly infested, the slugs collect under the bean piles in the fall and deposit many eggs. In the fall of 1917 more than five hundred slugs were taken under a pile of this kind, and the eggs were

countless. Slugs thrive in sod land and many eggs may be found in the spring around the roots of grass in fence corners and in meadows.

One pair of field gray slugs may deposit from 500 to 800 eggs, according to Theobald (1905). This writer says that the eggs are given out in batches of about 50 at a time, cemented together in piles of from 6 to 15. Taylor (1907) cites a case in which a pair of *agrestis* deposited 774 eggs during the season, and Lovett and Black (1920) found 612 eggs deposited by one specimen between May and the following April. One slug, found by the writer early in the spring, deposited 180 eggs between May 5 and June 19. Two slugs confined in one cage have produced as many as 464 eggs before they died, and it is probable that, due to cage conditions, this was less than the normal number.

Many eggs of *A. agrestis* do not hatch. After the severe winter of 1917, the writer was unable to find a single egg in the spring where there had been thousands in the fall preceding. This natural destruction is, without doubt, a great help in reducing the numbers of the pest in western New York. While the eggs need moisture for their development, excessively wet surroundings are unfavorable, for under such conditions they become moldy and spoil tho they may retain their normal shape. In a dry environment, the egg covering will shrivel and the egg will contract until it might be mistaken for a particle of the dirt on which it rests. When moisture is added, however, it will again swell to normal size. Bland and Binney (1873) describe experiments in which eggs of *A. agrestis* were dried many times in a desiccator, in some cases being kept in this condition for several years; when these eggs were again placed in normal moist surroundings, they assumed their usual shape and hatched. Since the development of the embryo in the egg is easily observed, much study has been given to this part of the life cycle by Mark (1881), Kofoid (1895), and Byrnes (1899).

The young slug

Newly hatched specimens of *Agriolimax agrestis* differ but little in their habits from the full-grown slugs. Because of the limited food supply in proportion to the large number of slugs hatching from a single egg mass, these slugs appear gregarious. As they become older and more hardy, they migrate from the original center and spread out in search of other food. Cooke (1895) reports that on hatching they go into the ground for four or five days before feeding. The writer had noted that green food in cages did not show strong evidence of feeding for several days after the slugs hatched, but he had attributed this to the small size of the radula, or rasping organ, at this time.

The young slug often secretes its slime in such large quantities that it is able to descend from plants to the ground on a thread of this material. Taylor (1907) states that this slime thread is the same as the trail left by the slug wherever it crawls, except that it is freed from contact with the

earth. The same writer declares that *agrestis* is able to descend at the rate of five inches a minute on a thread of this kind, and that one specimen was found hanging on a thread seven feet from the point of attachment. At times they reascend by this same thread.

The full-grown slug

The adults of *Agriolimax agrestis*, as well as the young, are nocturnal. They are seen during the day only in cloudy or rainy weather, or in shady and concealed places. In an infestation under observation on July 13, 1918, the slugs were on the plants from seven o'clock in the evening until eight in the morning. As it becomes light, the slug crawls into a crevice of the soil or under some protective covering such as grass, straw, or boards. This aversion to light is said to continue even after the eye-bearing tentacles have been removed. In a bean field the slugs frequently burrow down near a bean plant and feed on the parts below ground. The writer has found them buried from four to eight inches deep in the soil, with their tentacles drawn in. They were contracted and inactive, and were covered with a coating of slime to which particles of dirt adhered. In the cold weather of winter they hibernate in this resting position.

The field gray slug moves by an almost imperceptible shortening and lengthening of the muscles of the foot, or under side of the body. Taylor (1907) declares that two inches a minute is a good speed for this species, and has estimated that at this rate it would take twenty-two days and ten hours of steady movement to cover a mile. Since the slugs have been in this country they have apparently absorbed some of the American spirit, for they have been observed to go much faster than this. Some slugs are reported to return to the same hiding place night after night, but *agrestis* apparently does not have this habit.

The nocturnal travels of the slug are recorded each morning by the trail of slime which the animal leaves wherever it goes. After a rain these slime trails are often found on sidewalks, and in heavily infested fields the writer has seen the ground and the plants so coated with this glistening secretion that they have an iridescent appearance. More slime is secreted on a dry surface than on one that is moist, and on the dry surface the slime appears more milky, due, it is believed, to the presence of particles of carbonate of lime. This mucous secretion is supposed by some writers to aid in locomotion, while other writers declare that it regulates the evaporation, thus controlling the body temperature. It is thought also to serve as a protection against enemies. When irritated by a finely pulverized substance, such as lime, *agrestis* will give off large amounts of slime from the pores of its body, and when this mixes with the powder it usually forms a coat around the animal. The slug is sometimes able to escape by leaving this coat behind, but it may become so weakened by its struggles that it dies within the covering.

Method of feeding

Agriolimax agrestis does not eat in the same manner as does a biting insect, for its feeding apparatus is very different. The jaw (Plate LXIX, 10) is a concave, chitinous process attached to the roof of the pharynx. In the center it bears a tooth with finely serrate edges, which helps in tearing food apart. Opposed to this, on the floor of the pharynx, is a flexible plate made up of many small, sharp teeth, known as the radula (Plate LXX, 1, and fig. 92, A, page 981). This radula, or lingual ribbon as it is sometimes called, is supported on the muscular tongue and may be moved forward and backward. By the combined use of jaw and radula, small particles of food are torn from a plant and are then passed on to the stomach. Cooke (1895) states that the teeth of the radula are sharp enough to break the skin of the human hand if the slug is permitted to use this organ for a short time in one place.

Mating and oviposition

It has been previously noted that *Agriolimax agrestis* is hermaphroditic, both male and female sexual organs being found in the same individual. Whether or not the slugs are capable of self-fertilization is not definitely known. Theobald (1905) says that self-fertilization is rare, and that the male and female reproductive organs mature at different times. In the winter of 1917–18 the writer isolated specimens of *agrestis* a few days old and kept them in breeding jars in the insectary. One slug, on reaching maturity, deposited a few eggs; but because of an accident to the heating plant at a time when the temperature was far below zero, these eggs were frozen. Since that time it has been impossible to obtain eggs from isolated specimens, and therefore it cannot be said whether eggs of this type are fertile.

On the evening of July 7, 1920, the writer saw for the first time the sexual union of *A. agrestis*. Two specimens, one much larger than the other, were crawling around and around each other on a patch of slime about an inch in diameter. Sometimes they would strike each other with their tentacles. Soon the excitatory organ, or sarcobelum, was extruded, and this also was used in a caressing manner. After this behavior had continued for about three-quarters of an hour, the sarcobelum of each slug enlarged very greatly; the two organs came together and there was a great discharge of slime. In regard to the actual transfer, Taylor (1907:107) says, "The seminal element, mixed with mucus and worked up into a little ball, is transferred bodily, the forerunner of a true spermatophore."

Time required to reach maturity

In ordinary years, under field conditions in New York, slugs that have developed from eggs hatching in May are ready for oviposition in October

of the same year. This makes the time to sexual maturity about five months. In the wet season of 1917 this period was shortened to three months for some individuals. When the slug overwinters, it may be more than twelve months before it begins to deposit eggs.

Many specimens of *Agriolimax agrestis* that hatch in the spring do not live thru the following winter under New York conditions. In no case have slugs under observation lived thru two winters. This would make the greatest length of life actually observed in New York about eighteen to twenty months.

In European writings it is stated that *A. agrestis* may live for several years (Theobald, 1895); also, that the slugs are sexually mature in six weeks, and that there may be several generations in a year (Reh, 1913). Cooke (1895) reports that slugs of this species are usually full-grown by the middle of the second year and die during the first part of the third year. Taylor (1907) cites one instance in which a slug mated and deposited eggs in sixty-six days, was full-grown in eighty-two days, and lived for about eighteen months. The same writer states that the time from hatching to maturity probably varies from ninety days to nearly one year.

NATURE OF OUTBREAKS

When the outbreaks of *Agriolimax agrestis* occurred in 1917, it was noted that ordinarily the bean fields were evenly attacked. All the plants showed some injury to leaves and vines, but only a few were completely destroyed. The exception to this was in a field where a large tree, with its border of sod, seemed to act as a center from which the slugs migrated. In the grass near this tree were found many eggs and adults of *A. agrestis*, showing the place to be the local seat of infestation.

Only one outbreak of *agrestis* was observed by the writer in New York in 1918, and that was in Monroe County, in a slightly rolling field where the knolls had been covered with horse manure in the preceding fall. This field had been in sod for several years. The infestations seemed to start from the knolls, and when the field was seen by the writer the plants had been entirely destroyed as far as the slugs had migrated (fig. 92, C, page 981). Leaves and vines were completely devoured and the parts below ground were also attacked. The infested area grew larger each night as the slugs moved forward along the rows. In this infestation slugs of all sizes were present; the larger ones (40 millimeters) were in the front ranks of the advancing hosts, while far back in the devastated part of the field were the small ones (4 millimeters), which had been left behind in the rapid advance. This variation in size is unusual in New York and was probably the result of the exceptionally good hibernating place provided by the manure and sod of the field, which no doubt has allowed more or less continuous development thruout the winter.

RELATION OF AGRIOLIMAX AGRESTIS TO MOISTURE

Agriolimax agrestis is a moisture-loving animal. It is found above ground in large numbers only after rains or on cloudy days when the relative humidity is high. In 1916 and 1917, which were damp years at Perry, the slugs of this species were unusually active in the bean fields. During the past three years there have been no extensive, general outbreaks. From an examination of the relation of the rainfall of the past four years to the abundance of the slugs, it would seem that rainy weather in May and June, when the eggs are hatching and the young slugs are beginning their growth, makes conditions most favorable for their development. Especially is this true if two or more such years come in succession. In 1916, and again in 1917, these months were rainy. In June of 1916 the rainfall at Rochester, New York, was 5.72 inches, and for the same month in 1917 it was 6.40 inches; while in 1918, 1919, and 1920, it was below the monthly average of 3.13 inches.

It sometimes happens, after a rainy period, that the ground dries and bakes so hard that the slugs cannot break the hard crust and are thus forced to feed below the surface. On heavy, undrained soils the damage is always greater than on lighter ground. Since the growth of the slugs is dependent on the amount of food eaten, and since their feeding is heavier in moist surroundings, it is easy to see why they mature much more quickly in moist than in dry seasons. During dry periods the slugs are found deep in the soil, in contracted positions. They work their way far below the surface of the soil in search of moisture. Reh (1913) says that a slug supplied with plenty of moisture after having been under dry conditions, may become three times as large as it was before.

RELATION OF AGRIOLIMAX AGRESTIS TO EXTREMES OF TEMPERATURE

The field gray slug can survive cold weather if it is in a protected position; but a temperature of 14° F. proved fatal to specimens in flower-pot cages in the insectary at Ithaca when there was no fire in the building for several days. Few slugs survived the unusually cold winter of 1917–18, as was shown by the fact that in the spring of 1918 the writer could find but a small number in the fields near Perry where there had been thousands in the fall preceding. The slugs that had escaped the cold had done so by crawling under the sod and the rubbish in fence corners or other protected places. Very few of the millions of eggs deposited under the bean piles in the fall of 1917 survived. These occasional severe winters are believed to have an important influence in keeping down the numbers of this pest in New York. January of 1918 was the coldest January, as well as the coldest month, within the scope of the official weather records. The mean monthly temperature for that month at Ithaca was 9.7 degrees

(Fahrenheit) below the normal. The first half of February was also unusually cold. Since that year slugs have been so scarce that injury to beans caused by them has been almost unheard of.

In the study of the distribution of *Agriolimax agrestis*, it may be noted that it has not been reported as serious in the Southern and Middle Western States. This is perhaps because the high, dry temperatures of these States during the summer are unfavorable to its successful development.

SEASONAL HISTORY

In western New York there is normally but one generation of *Agriolimax agrestis* in a year. Sometimes the eggs deposited in the fall hatch in the following spring, and the slugs from these eggs are full-grown by August and, in their turn, deposit eggs from September to December. These adult slugs usually die before the next spring. Sometimes, however, full-grown slugs live thru the winter and deposit their eggs in May and June of the next year. These spring eggs hatch at about the same time as the overwintering eggs.

PREDATORY AND PARASITIC ENEMIES

In England, acording to Theobald (1905), slugs are preyed upon by the thrush, the starling, the pigeon, the blackbird, the duck, and poultry, as well as by the toad, the shrew, the mole, and the centipede. Ritzema Bos (1890) states that in France, beetles of the families Carabidae, Staphylinidae, and Lampyridae feed on slugs; and Cooke (1895) reports that there is a fly which lays its eggs with those of *Agriolimax agrestis*, and that the slug is parasitized by the larva. The same writer says also that nematodes likewise help to reduce the numbers of these slugs. Banks (1915) reports that a mite (*Eryngates limacum* Koch) has been found attached to some species of slugs.

In western New York, chickens free to run in the fields have eaten many slugs. Eggs of the species in a wet petri dish were found to have nematodes feeding in them. The small worms would apparently make a hole thru the outer covering of the egg and feed on the embryo within.

CONTROL

Various control measures against *Agriolimax agrestis* have been tried and recommended. In many cases advantage has been taken of the irritation and the secretion of mucus caused by finely pulverized and granular materials coming in contact with the slug. Lime, both air-slaked and hydrated, is the most commonly recommended of these irritants; other materials suggested are salt, caustic soda, tobacco dust, wood ashes, soot, road dust, hellebore, powdered coke, sawdust, and various combinations of these.

slugs are very often trapped by placing cabbage leaves, straw, culled potatoes, turnips, sacking, or shingles near their favorite haunts in the evening. In the morning they may be easily found and destroyed under these traps, where they have crawled to avoid the daylight. Poison baits of bran, chopped green leaves, drippings, and potatoes, mixed with arsenate of lead, white arsenic, arsenite of zinc, arsenate of calcium, or paris green, as the poison, are said to help in slug control. Fertilizers such as land plaster, nitrate of soda, potassium sulfate, and iron sulfate have been recommended, especially in European countries.

For killing *A. agrestis* by contact or for controlling the slug by a repellent, it has been advised that plants be sprayed with blue vitriol solution, with bordeaux mixture, with pyrethrum, or even with hot water; and as a poison, a spray of arsenate of lead or calcium arsenate is suggested.

It is thus evident that many methods of control have been advised, some of which may work well in a small garden. In a bean field of ten acres or more, with an even infestation thruout, the problem is one of greater complexity.

Experimental work

When this study was begun, in the summer of 1917, the easiest method of control appeared to be the application of a poison spray to the plants. Experiments along this line were started on July 17. Several rows were

TABLE 7. CONTROL EXPERIMENTS AGAINST *AGRIOLIMAX AGRESTIS*

Material applied	Effect on slugs
Very fine tobacco dust	Dead in 15 minutes
Coarse tobacco dust	Not killed
Builder's lime	Dead in 5 to 15 minutes
Dry powdered bordeaux (dust)	Dead in 5 to 60 minutes
Tobacco dust, sulfur, arsenate of lead (1 :5 :1	Dead in 15 minutes
Sulfur (finely ground)	Not killed
Copper sulfate (10-per-cent solution	Dead in 15 minutes
Copper sulfate (5-per-cent solution	Dead in 40 minutes
Copper sulfate (2-per-cent solution)	Not killed
Sulfocide (5 cc. to 500 cc. of water)	Not killed
Lime-sulfur (1-20 solution)	Not killed, irritation caused
Black-leaf-40 (1 cc. to 500 cc. of water)	Dead in 2 hours
Quassia solution (hop-aphis formula)	Not killed
Lime (air-slaked)	Dead in 3 to 20 minutes
Washing soda (dust)	Dead in 10 minutes
Chloride of lime (dust)	Dead in 15 minutes
Washing soda (1 pound in 3 gallons of water)	Not killed
Chloride of lime (1 pound in 3 gallons of water)	Dead in 2 hours

sprayed with a mixture of 3 pounds of powdered arsenate of lead to 50 gallons of water. No difference could be noticed between the sprayed and the check plots when they were examined some time later. Slugs were placed also on sprayed plants in cages. Feeding was noticed on the leaves but the animals were not killed. In the greenhouse, in December of 1917, a slug devoured two heavily sprayed plants and lived for many days. From these data it seems evident that ordinary doses of arsenate of lead do not kill *Agriolimax agrestis*.

The experiments summarized in table 7 were carried on in the insectary at Ithaca during the winters of 1917 and 1918. The slugs were sprayed with the liquid or were dusted lightly with the powder, after which they were returned to natural conditions, on moist earth in an open jar.

It may be seen from table 7 that under insectary conditions many dusts proved effective. Copper-sulfate solution also showed strong killing power. It was noticed at this time that a 10-per-cent copper sulfate solution, sprayed on a piece of paper and allowed to dry, was very irritating and sometimes fatal to a slug that crawled across the paper. Lime, chloride of lime, and washing soda were more effective in the form of dust than in the liquid form. Approximately ten slugs were used in each test.

The experiments summarized in table 8 were likewise conducted in the insectary during the winters of 1917 and 1918. Bean plants growing in a bench, and also the ground close to them, were treated with the various liquids and dusts, and a cylinder open at the top was placed over them.

TABLE 8.—CONTROL EXPERIMENTS AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Hydrated lime water (1 pound to 3 gallons)	1 killed, 1 kept from plant for one week
Stone lime (1 pound in 2 gallons of water)	Killed in trying to reach plant
Bordeaux (4-4-50)	Chose unsprayed in preference to sprayed leaves
Arsenate of lead (2 pounds in 50 gallons of water)	Alive after eating two plants
Arsenate of lead, as above, sweetened with molasses	Molasses injured plant
Calcium arsenate (1-50) and sulfocide	Slug not killed, little feeding
Calcium arsenate (1-50) sweetened	Molasses injured plant
Sodium arsenate (10 grams in 1 gallon of water)	Slug alive, plant killed
Check (sprayed with water)	Slug alive
Kansas grasshopper bait	3 of 4 slugs alive 1 week later
Salt and lime (1-10)	Slug killed in 24 hours
Iron sulfate (10-per-cent solution)	Plant killed
Arsenate of lead and lime (1-8)	Slug kept from plant for 1 week
Hellebore and lime (1-25)	Slug killed in 2 hours

One or more slugs were then placed in the cylinder at some distance from the treated plant.

In the experiments summarized in table 8, the repellent effect of bordeaux mixture is shown. Hellebore and lime, as well as salt and lime, showed some killing power under insectary conditions. Calcium arsenate and lead arsenate when sweetened with molasses were fatal to the bean plants, and the ineffectiveness of arsenate of lead as a stomach poison of *A. agrestis* is shown.

In the summer of 1918, contact substances, in powder form, were tried against *A. agrestis* near the field laboratory at Perry. The material was dusted lightly on the slug with a Niagara duster and the animal was then returned to natural conditions. Five slugs were used in each test. The results of some of these experiments are given in table 9:

TABLE 9 EXPERIMENTS WITH POWDERED-CONTACT SUBSTANCES AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Superphosphate	Killed slowly if extensively used
Rock phosphate	Killed slowly if extensively used
Acid phosphate	Killed slowly if extensively used
Basic phosphate	Not killed
Land plaster	Not killed
Fine ground bone	Not killed
Sulfate of potash	Killed quickly
Nitrate of soda	Killed quickly
Dried blood	Not killed
Ground limestone	Not killed
Calcium cyanamid	Killed rather slowly
Kainit	Killed quickly
Salt	Killed quickly
Sulfur	Not killed
Fine tobacco dust	Killed slowly if extensively used
Chloride of lime	Killed very quickly
Air-slaked lime	Killed quickly
Water-slaked lime	Killed quickly
Salt and lime (1 10)	Killed very quickly
Hellebore and lime (1 10)	Killed very quickly
Hyposulfite of soda	Killed slowly

The nitrate of soda and the kainit proved injurious to the plants when tested in the field. Of the dusts that were not injurious to the plants, as recorded in table 9, the salt-and-lime and the hellebore-and-lime combinations, and the chloride of lime alone, acted the most rapidly, altho some of the other materials also showed killing power.

Liquid-contact materials also were tested in 1918, as shown in table 10. While the slug was crawling on the ground it was sprayed with the liquid from an atomizer, and was then left under natural conditions.

TABLE 10. LIQUID-CONTACT SPRAYS TRIED AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Black-leaf-40 (1 400), soap (4 50)	Killed slowly but surely
Limewater (2-per-cent solution	Killed
Chloride of lime (2-per-cent solution	Killed quickly
Kerosene emulsion (10 per cent)	Not killed
Kresco sheep dip (10 per cent	Killed
Carbolic emulsion (1 20)	Killed
Copper sulfate solution (5 per cent	Killed slowly

In the experiments summarized in table 10, ten large slugs were used to test each material. The Black-leaf-40 was fatal every time, but it often required several hours to kill the slug. The limewater, the chloride of lime, and the carbolic emulsion proved fatal in thirty minutes. The copper sulfate seemed to work much more slowly than in the former tests.

In 1918, during an outbreak at Charlotte, New York, a poison bait composed of one quart of chopped clover, one teaspoonful of arsenate of lead, and one tablespoonful of molasses, was tested. The slugs showed no preference for this bait, and several specimens that were placed where the bait was the only food available, and thus forced to eat it, were not killed.

In July, 1920, the writer was able to find a sufficient number of slugs to enable him to conduct a small series of laboratory tests. The result of these are given in table 11.

In the experiments of 1920, recorded in table 11, both full-grown and immature slugs were used. It was noted that the larger individuals often revived from doses that proved fatal to the smaller specimens. Control materials in dust form seemed to give much better results at this time than did the same material applied as a liquid. In previous experiments sprays have sometimes seemed to give as favorable results as the dusts. There is apparently some varying factor that enters to either help or hinder the killing power of some of these materials. It is possible that the relative humidity may have some influence. Black-leaf-40, which had shown good killing power in the previous experiments, seemed to act very slowly even at the increased strength that was used. Carbolic-acid emulsion gave satisfactory results, and when applied to bean foliage it caused no injury under the prevailing conditions. The best results at this time came from

the contact dusts, but when lime was applied to slugs in the field it was necessary to use several doses before killing resulted. The slug would give off the usual slime, which would mix with the lime to form a coat from which the animal soon freed itself. Heavy doses often killed when light applications did not.

TABLE 11. CONTROL MATERIALS TESTED AGAINST AGRIOLIMAX AGRESTIS IN 1920

Material and strength	Number of slugs	Effect on slugs after 18 to 24 hours
Liquids:		
Black-leaf-40 (1-250), soap (1-100)	25	Small slugs killed if sprayed heavily; large ones revived
Black-leaf-40 (1-250), glue (1 pound to 50 gallons)	10	Small slugs killed, a few large ones revived
Glue (4 pounds to 50 gallons of water)	10	Not killed
Black-leaf-40 (1-250), lime (1 pound to 3 gallons) (light dose)	10	Sick, but all except one revived
Same (heavy dose)	10	All killed
Hydrated lime (1 pound to 3 gallons of water) (light dose)	10	All alive next day
Air-slaked lime (1 pound to 3 gallons of water) (heavy dose)	10	Two large slugs alive; remainder dead
Same (light dose)	10	Five large slugs alive
Lime (1 pound to 3 gallons of water, salt (1.6 ounces to 3 gallons)	10	Five large slugs alive
Lime (8 ounces to 3 gallons of water, chlorinated lime (1.6 ounces to 3 gallons	10	One large slug alive
Lime (8 ounces to 3 gallons of water, caustic soda (1.6 ounces to 3 gallons)	10	Four large slugs alive; plants burned
Chlorinated lime (8 ounces to 3 gallons of water)	10	Five slugs alive
Carbolic emulsion (diluted 1-30)	10	Killed quickly
Lye (2 pounds to 50 gallons of water)	10	Killed quickly, plants killed
Resin caustic soda wash (28.3 g. resin, 3.5 g. caustic soda, 645 cc. water)	10	Four small slugs killed
Dusts:		
Hellebore and lime (1-25)	10	All dead
Chlorinated lime and lime (1-25)	10	All dead
Hydrated lime	10	All dead
Niagara Sprayer Company's "All-in-One"	10	All dead
Water-slaked lime	10	All dead
Salt and lime (1-10)	10	All dead
Caustic soda and lime (1-20)	10	All dead
Sulfate of potash	10	All dead, plants burned
Calcium cyanamid	10	All dead, plants burned

Three field cages, containing bean plants sprayed, respectively, with powdered arsenate of lead (2 pounds to 50 gallons of water), calcium arsenate (1 pound of the powder to 50 gallons of water), and water alone to serve as a check, were set up in the laboratory field in July, 1920. Twenty slugs were placed in each cage. The plants sprayed with arsenate of lead were freely eaten, as had been the case in previous experiments, but those sprayed with calcium arsenate showed little evidence of any feeding after the first two days. Several dead slugs were found in the calcium-arsenate cage, while none were found in the arsenate-of-lead cage. The check plants, sprayed with water only, were almost entirely destroyed. The scarcity of slugs in the field had made it impossible to test the calcium-arsenate spray on a larger scale.

A cage was placed in the field covering eight bean plants on July 7, 1920. Four of these plants were sprayed with bordeaux mixture and four were left unsprayed. Twenty slugs were then placed in the cage. A week later the unsprayed plants were badly eaten, while the sprayed plants were almost untouched. Only where a leaf had been missed by the spray was it injured.

Since the above work was carried on, the excellent paper of Lovett and Black (1920) has come from the press. As a result of many careful experiments, these writers conclude that, for Oregon conditions, a spray of bordeaux mixture (4–4–50) as a repellent, supplemented by a poison bait of calcium arsenate (one part by weight to sixteen parts of chopped lettuce), is the most effective means of slug control. When lettuce is not available, cabbage, kale, clover, or other succulent leaves may be used. The writers say that this bait should be scattered in small heaps at frequent intervals over the infested area. The importance of cleaning up crop remnants and débris about fields and gardens is also emphasized. In an experiment testing the efficiency of this combination of repellent and poison bait, Lovett and Black found 33 out of 35 slugs dead at the end of twenty-four hours. The bordeaux had kept the slugs from the plants and they were killed by feeding on the poison bait.

As previously stated, the severity of the winter of 1917–18 apparently killed many hibernating slugs and many slug eggs. Few slugs have been found in New York bean fields since that time, and the writer has not found conditions favorable for control experiments in the field. In 1920 there were more slugs in bean fields than in the two preceding years, but very little injury resulted. The control work has therefore been limited to field-laboratory and greenhouse experiments carried on whenever slugs were available. Results of laboratory experiments have at times been contradictory, and, since laboratory control measures often prove entirely inadequate in field practice, it is impossible at this time to do more than suggest possible control measures for field use under such conditions as those of western New York.

The repellent quality of bordeaux mixture appears to be definitely established. Plants sprayed with bordeaux have escaped all injury when unsprayed plants were entirely devoured. It has been demonstrated by Lovett and Black (1920) that calcium arsenate also has great killing power when used in a poison bait, and the writer found dead slugs in a cage in which the beans had been sprayed with this material. It is therefore reasonable to suppose that a spray of calcium arsenate may be effective under field conditions.

Dusts of lime, salt and lime (1-25), hellebore and lime (1–25), and chloride of lime and lime (1-25), show some promise of success, and on a small scale should work especially well.

A very helpful practice, both in field and garden work, is to remove all rubbish and crop remnants from the ground. Old bean and potato vines, cabbage stumps, carrots, turnips — in fact, decaying vegetation of any kind which may furnish either food or shelter for the slugs — should be cleared away. Straw, boards, roots of quack grass, piles of leaves, and manure, have been found to harbor many of the pests. After a slug infestation, crop remnants should be plowed under or removed from the field as soon as the crop has been harvested. It is advisable also to clean up the edges of gardens and fence corners in the fall if slugs have been abundant during the summer, for the greatest injury to the plants is that caused by slugs hatched from the eggs deposited by overwintering slugs that have hibernated in these places. After the grass and the weeds have been cut and the rubbish has been removed, the application of a heavy coating of lime or salt to the ground helps to destroy the animals.

Beans grown in fields that were in sod the preceding year are often infested. Covered by the roots of the grass, the slugs and their eggs have been well protected during the winter, and when spring comes they find an abundant food supply in the newly planted beans. If manure is added in the fall to sod land in which slugs are present, it makes hibernating conditions even more ideal.

Summary of control suggestions

Bean plants should be thoroly sprayed with bordeaux mixture (4–4–50) to keep the slugs from them. The plants should be sprayed from both above and below, preferably with a potato sprayer having three nozzles to a row. Unless the infestation is severe, this spray should be sufficient. In severe attacks, however, the bordeaux mixture may be supplemented by a bait of chopped lettuce or clover, 16 parts by weight to 1 part of calcium-arsenate powder, the mixture to be scattered around the field. This bait should attract and kill slugs driven from the plants by the bordeaux. As an experiment, the bean foliage may be sprayed with calcium arsenate, 1 pound to 50 gallons of water. In a small garden the slugs

may be collected at night, by the light of a lantern; cabbage leaves, shingles, or straw may be used as traps, from which the slugs may be collected in the morning and destroyed. All crop remnants and rubbish should be carefully removed from infested areas in the fall and destroyed, and salt or lime should be scattered around the edges of the infested fields or gardens. Manure should not be placed on infested fields or gardens in the fall.

HOW TO DISTINGUISH THE VARIOUS SPECIES OF SLUGS FOUND IN BEAN FIELDS

There are three slugs that the writer has frequently found associated with *Agriolimax agrestis*. They are *Agriolimax campestris* Binney, a native species, and *Limax maximus* L. and *Arion circumscriptus* Johnson,[1] imported species. The following key may help in distinguishing the four species.

A. Body blunt or rounded at posterior end, respiratory opening in anterior half of mantle; back not keeled in mature forms; color gray, with a black lateral band the entire length of body; length 30 mm. ..... *Arion circumscriptus*

B. Body pointed at posterior end; respiratory opening in posterior half of mantle; back with at least a small keel at posterior end; color varied, but without the single lateral stripe.

a. Slug large (100–200 mm.); spotted or with longitudinal bands of black. ..... *Limax maximus*

b. Slug smaller (25–50 mm.); color uniform or mottled.

aa. Ground color usually whitish or ocherous, mottled or speckled with brown or black; mantle pore with unpigmented border; tubercles flattened; slime milky; length when full-grown, 50 mm. ..... *Agriolimax agrestis*

bb. Color uniformly amber or black; mantle pore of same color as remainder of mantle; tubercles not flattened; slime watery; length when full-grown, 25 mm. ..... *Agriolimax campestris*

Agriolimax campestris Binney

Animal limaciform, with large, not flattened, tubercles. Color uniform gravish or amber often black. Body somewhat compressed and keeled toward the caudal end. Tentacles dark-colored. Shield more than one-third total length of animal, rounded in front and behind. Respiratory orifice not differing markedly in color from remainder of mantle. Sole dark and longitudinally tripartite. Mucus clear and watery. Penis spiral. Length about 25 mm.

Agriolimax campestris, a native species, is closely related to *A. agrestis*. It differs from *agrestis* in being smaller, darker, and of a more uniform coloring. While *agrestis* seems to collect in large numbers and to thrive on cultivated crops, *campestris* is more inclined to be solitary and to frequent woods and meadows. In April, full-grown *campestris* are often found under stones or in sod, and the eggs have been found at the same time. Eighteen of these eggs, taken on April 22, hatched between May 21 and June 1. The young of *campestris* are darker than the young of

[1] Determined by H. A. Pilsbry.

agrestis, some being almost black. It is not uncommon to find *campestris* feeding on beans, but they never occur in numbers large enough to seriously damage the crop.

The spotted garden slug, Limax maximus L.

Limax maximus (Plate LXX, 6), is described by Taylor (1907:35) as follows:

Animal with a long and slender body, tapering towards the tail, and varying in length from 100 to 150 mill., but occasionally reaching to even 200 mill., usually of a yellowish-grey or cinereous ground colour, variously banded or maculated with black, but sometimes unicolorous; body rounded, but keeled towards the caudal end, with about forty-eight longitudinal rows of elongate, detached tubercles, neck pale, with two conspicuous dorsal furrows enclosing a single row of elongate tubercles and terminating in front as the facial grooves; sole uniformly pale, foot-fringe pale with a row of minute submarginal blackish tubercles; tentacles very long and slender, shield oblong, about one-third the total length of the animal, rounded in front, angular behind, and forming an angle of about 80 deg. when in motion, usually of a similar tint to the body, but boldly marbled or maculate with black, somewhat concentrically and interruptedly ridged around a sub-posterior nucleus. Mucus colourless and iridescent, not very adhesive.

Limax maximus is a large slug, of the family Limacidae, which has been imported into this country. It is found in the British Isles, and thruout Continental Europe, South Africa, and Australia. It has been in America for many years and may be found locally in many parts of New York State, where it frequents greenhouses, hedgerows, woods, and damp, shady places. It occurs also in and around houses occasionally, when it has been carried in on vegetables that are stored in the cellar. Taylor (1907) states that the slug is almost omnivorous, having been known to relish beans, tobacco, flowers of many kinds, cauliflower, fungi, custards, milk, bread, raw and cooked meat, fruit, and sugar.

L. maximus has a keen sense of smell. It has been known to crawl, in the dark, straight to a plate of meat that was six feet away. The position of the plate was then changed three times, and each time the slug altered its course accordingly. It is said that *L. maximus* often returns to the same spot night after night, after its wanderings in the dark. The progress of the night's journey is shown by the slime trail which is left wherever the animal goes.

Arion circumscriptus Johnson

The following description of *Arion circumscriptus* (Plate LXIX, 12) is taken from Taylor (1907:228):

Animal of the *Arion* shape, but stouter especially when contracted, about thirty mill. in length when adult and fully extended, of a pale creamy-grey colour, darker grey dorsally, the shading to whitish towards the fringe, a black and sharply-defined lateral band extends the whole length of the body on each side, beneath which is sometimes an indistinct orange band formed by pigment cells breaking through the skin, there is a slight mid-dorsal keel in young, which, however, gradually disappears during growth, but its place is almost

invariably indicated by a line of pale mid-dorsal tubercles, which contribute to form a pair of dorsal or inner bands; shield granulose and bluntly rounded at both ends, bearing a disconnected continuation of the longitudinal body banding; body tubercles rather long and slender; sole opaque, waxy white, and indistinctly tripartite, the median portion slightly darker and more transparent than the side areas, and occupying more than one-third of the width of the body, foot-fringe broad and white or pale-grey in colour, usually without perceptible lineolations, but sometimes the lineoles are clearly pigmented, especially at the caudal end of the body

Another slug occasionally found with *Agriolimax agrestis* in New York is *Arion circumscriptus* Johnson, a species imported into this country from Europe and reported by Taylor (1907) from Niagara Falls and from the District of Columbia. The writer has found it very common at Ithaca, at Perry, and at Waterville, in New York. This slug apparently prefers to live in sod land, in decaying tree trunks, or under fallen leaves. It may be found in grassy orchards, feeding on bruised and decaying fruit. It is seldom, if ever, injurious to growing plants. The species belongs to the family Arionidae. It may be easily separated from the other slugs found with *Agriolimax agrestis* by the position of its respiratory pore, which is in the anterior half of the mantle while in the other forms it is in the posterior half. A longitudinal black band runs the full length of the animal's body.

THE PALE-STRIPED FLEA BEETLE

(*Systena taeniata* Say)

The pale-striped flea beetle, *Systena taeniata*, of the family Chrysomelidae, is found in the bean fields in New York State every year, in large or small numbers. This small, active insect is brownish yellow in color, with a broad yellow stripe running lengthwise along each wing cover (Plate LXIX, 11). There are several color varieties of the insect, but the common one in New York is *blanda*, in which there is little contrast between the stripe and the remainder of the wing cover. The typical dark form is found occasionally. In early writings these varieties were often treated as separate species. When *S. taeniata* is numerous in dry summers, the beetles may cause considerable injury to beans by attacking the foliage. They leave in their wake many shallow feeding places on the surface of the leaves, and some of these spots later develop into irregular holes. If the plant is unable to supply sufficient soil water for the increased transpiration resulting from the injury, the leaves will turn a sickly yellow. In a year when the normal supply of soil moisture is available, beans can sustain much damage from the feeding of the insect without any serious injury resulting to the development of the plant.

S. taeniata is a well-known insect in nearly all parts of the United States, and in many places is considered a serious pest. It has injured sugar beets in Michigan, in New York, and in Colorado, corn in Illinois, clover in Kentucky,[1] cotton in Georgia, Kieffer pear grafts in Maryland, and seedling apple trees in New York. Other host plants of the insect are

cabbage, potato, pea, tomato, pumpkin, melon, squash, cucumber, turnip, radish, carrot, eggplant, strawberry, blackberry, lettuce, sweet potato, summer savory, peanut, sunflower, oak, timothy, and oats. It is reported by Chittenden (1900) and other writers as occurring also on the following weeds: ragweed, lamb's-quarters, pigweed, Jamestown weed, cocklebur, black, or garden, nightshade, purslane, fleabane, sand bur, and other plants. The writer has found it on mustard and daisy.

Every time that *S. taeniata* has been found on beans in New York, some of its common weed hosts have been near by. Ragweed and lamb's-quarters appear to be its favorite food plants.

DESCRIPTION OF STAGES

The egg

The egg of *Systena taeniata* (Plate LXX, 3) is elliptical, slightly more rounded at one end, is pale yellow in color, and has a roughened surface. Under the high power of the microscope, the egg covering is seen to be divided into a definite pattern of depressed hexagonal areas, with irregular reticulations in the hexagons. Under a lens it appears faintly roughened. Its length is from 0.6 to 0.65 millimeter.

The larva

The larva (Plate LXIX, 8) is described by Forbes (1894) as follows:

Length 5 mm., greatest width about .6 mm. Slender, widening gradually to the 11th segment, thence tapering quite rapidly. General color pale yellow or brownish yellow, paler towards the posterior end. Head yellowish brown, with numerous stiff hairs; jaws darker brown. Antennae three-jointed, pale, short, and thick. The thorax and abdomen are darkest on the dorsum, fading to paler on the margins and ventral surface, and the latter very pale yellowish at the end. The first thoracic segment has two longitudinal curved impressed lines on the dorsum; segments two and three have longitudinal impressed lines on each side near the border, between which is a transverse curved line crossing each segment near its anterior margin, from which two oblique straight lines extend to the posterior margins of the segments. The legs have stout, blunt, spine-like processes on their anterior surfaces, and stiff hairs on the posterior. The abdominal segments are transversely wrinkled on both anterior and posterior margins. The skin is shagreened, and the whole body is supplied with stiff, spine-like hairs of various lengths. The anal segment has a single fleshy proleg. When seen from above this segment rapidly narrows to midway its length, the posterior half forming a rounded, lobe-like projection of about one half the width of the anterior portion of the segment. On the projection are four long, stiff, spine-like hairs and a marginal crown of shorter spine-like processes, each of which ends in a fine, curved, hair-like lash. (Described from two specimens.)

The pupa

The pupa (Plate LXIX, 9) is pale yellow in color until just before the emergence of the adult beetle, when the darker body markings may be seen thru the pupal skin. The end of the body bears two heavy, prominent, slightly incurving spines. The length is about 4 millimeters.

The adult

The adult (Plate LXIX, 11) is described by Blatchley (1910) as follows:

Elongate-oval. Color variable, usually reddish or brownish-yellow, shining; elytra every always with a paler median stripe, under surface and narrow margins of thorax usually piceous; antennae and legs reddish-brown. Thorax one-fourth wider than long, sides feebly rounded, surface finely and sparsely punctured. Elytra distinctly wider than thorax, finely, shallowly and rather densely punctate. Length 3–4.5 mm.

LIFE HISTORY AND HABITS

The egg

Eggs of the pale-striped flea beetle were nearly mature in dissected females on July 15, 1919, and beetles placed in a cage with ragweed and beans on that date had deposited eggs in the soil by July 22. In 1920 no eggs were found in females opened on June 29, but they were present in specimens opened on July 21. In the cages eggs were deposited for some time after August 6; many were deposited about August 25, and some could still be found on September 8. It may be said that in New York the period of oviposition of *Systena taeniata* extends from the last of July until the first part of September.

In 1919, after finding eggs of *S. taeniata* in cages the writer looked for them in the field, and on July 29 a few were discovered around ragweed. On August 5 some were taken near the roots of lamb's-quarters, and later many more were found around this host. Nineteen eggs under observation in the laboratory hatched in an average of 17 days, with a range from 15 to 23 days.

The egg of *S. taeniata* closely resembles that of *S. frontalis*, which is frequently present in the same habitat, and sometimes it is difficult to distinguish the eggs of these two species. However, the eggs of *taeniata* are smaller and are deposited earlier in the season than those of *frontalis*. Few females of *frontalis* were mature when eggs were found in the field on August 5, and, since a dead specimen of *taeniata* was found in the ground near these eggs, there is little doubt of their parentage.

Eggs of *taeniata* are usually scattered in the ground singly, but they may occur in clusters of from two to seven. They may be found from half an inch to three inches deep, and the writer has always found them near the roots of ragweed and lamb's-quarters tho they no doubt occur also near some of the other hosts of the insect.

The larva

Eggs of *Systena taeniata* have hatched in the laboratory from [illegible] 25 to September 8. The newly hatched larvae feed below ground on [illegible] roots of their weed hosts. A few small larvae, together with eggs of [illegible] species, were found on the lateral roots of lamb's-quarters in August, 1919. Larvae of this species have not been found feeding on the roots of bee

The writer has not succeeded in rearing these larvae, but it is believed that the insect hibernates in the larval stage near the roots of its host plants. On May 25, 1920, larvae of what is believed to be this species were found around ragweed, but when these were taken to the laboratory for rearing, they died. Later, pupae of *S. taeniata* were found in this same place. It seems reasonably certain, then, that the larval stage normally begins between the last of July and the middle of September, and does not end until late May or early June of the following year. This would make a larval period of from nine to eleven months. In 1886 Forbes (1894) found larvae feeding in young corn plants in Illinois on May 17, and again on July 11 and 12. Chittenden (1903) reports finding larvae feeding on the roots of lamb's-quarters and Jamestown weed.

The pupa

Pupae of *Systena taeniata* were found from June 29 to July 12, 1920, around dead ragweed along the edge of a field that had been in beans the previous year. Twenty were discovered about one plant, three inches below the surface, in rather compact soil. Beetles emerged from these pupae between July 13 and July 25. Forbes (1894) reports pupae emerging on May 26 and June 7 from larvae found on May 17. Adults from these pupae emerged by June 17. It would appear, then, that the pupal stage may cover from two to three weeks.

The adult

Pale-striped flea beetles have been taken in the field from the middle of June until the middle of September. In 1920 the first beetle was seen on June 19 and a few were alive in cages on September 10; the maximum number was present on plants about July 20. The ovaries of female beetles opened on June 29 were very immature, but many well-developed eggs were found in insects dissected on July 21.

It has been noticed each year that when *Systena taeniata* becomes scarce on beans, beetles may still be found on ragweed and lamb's-quarters, especially along the edges of fields. On August 19, 1920, *taeniata* was becoming scarce on beans, but it occurred in large numbers on its weed hosts until about September 3.

During the latter part of their adult life, the females go down into the ground around their favorite food plants to deposit their eggs. In searching for eggs, the writer has often found the beetles crawling in the dirt three inches below the surface. One much battered female was found four inches down in the ground, near a ragweed plant, on September 16, 1919, when most of the beetles had disappeared. On September 23, 1919, a beetle with particles of dirt adhering to its legs and its wing covers was found on ragweed. It had apparently been down in the ground, had deposited its eggs, and had come up again to feed.

The parent beetle of *S. taeniata* lives for a relatively long time and the period of oviposition covers a month or more. Beetles have been seen in copulation from June, when the ovaries were still immature, until September, when nearly all the eggs were deposited. Since the period of egg laying may vary so greatly, it seems likely that some beetles which emerge late in the summer and continue to oviposit for a long time may pass the winter in the beetle stage. Chittenden (1903) states that the insect hibernates as an adult, and Gibson (1913) found overwintering beetles in timothy fields in Ontario (Canada) in May. There is therefore good evidence of adult hibernation in some places, but the writer believes that this is rare in New York. Forbes (1905) believes that in Illinois the insect hibernates as a larva, and the writer's observations point to the same conclusion for New York. Chittenden (1900) believes that there may be a second brood at Washington, but the writer believes that in New York there is only one brood.

SEASONAL HISTORY

The parent beetle of *Systena taeniata*, emerging during June and July, deposits eggs in the ground around ragweed, lamb's-quarters, and possibly other hosts, from July to September. These eggs hatch in from two to three weeks, and the larvae hibernate after feeding for some time on the fine roots of their host plants. During June and July of the next year these larvae emerge as pupae, and after two or three weeks the beetles appear. In New York there is only one generation a year.

CONTROL

Clean cultivation is an important factor in the control of *Systena taeniata*. Fence corners and the edges of fields, which are never cultivated and where ragweed and lamb's-quarters flourish, often become centers of infestation. The pupae of *taeniata* have been found in large numbers around these weeds at the side of a field that had been in beans the preceding year. In this field the beetles were first seen near these weeds in the spring, and throughout the summer, when beans were again planted, the insects were more numerous along this border of the field. When the female beetles are mature they seek out these weed hosts as places for oviposition. The careful eradication of these weeds from the side of the fields and from among the bean plants will help greatly in reducing the numbers of the insect. Eggs are often deposited near weeds growing in the field proper, but it is probable that many larvae and pupae are destroyed when the ground is fitted for the following crop. If these weeds are removed from a field and from its environs late in August, when most of the eggs are deposited, the young larvae will be without food and many will die. One grower planted beans in the same field for several succeeding years and there were always many *taeniata* present on his plants. Early in the summer of 1919, he pulled out all of the ragweed and lamb's-quarters [illegible] the field proper, as well as that along the margin, and in 192[illegible] more

than one-fourth as many flea beetles were present as there had been the year before. The food supply of the young larvae was removed at a critical time, apparently causing many to die of starvation.

The parent beetles are often numerous on ragweed and lamb's-quarters growing among wheat and oat stubble in the fall; and it has been noticed that when beans were planted in these fields the following year, the beetles were often abundant. Beans grown on land that had previously been in clover in which some ragweed had also sprung up, often show as heavy an infestation of *S. taeniata*. If sod land or stubble land of this type is plowed deep in September, when the larvae are small, so as to destroy the larval food supply, it is probable that the infestation of the following spring will be much reduced.

Artificial control measures tested against *S. taeniata* and the red-headed flea beetle, *S. frontalis*, are discussed on page 1009.

FIG. 93.—BEAN PLANTS DAMAGED BY THE RED-HEADED FLEA BEETLE

A few beetles may be seen on the plants.

THE RED-HEADED FLEA BEETLE

(*Systena frontalis* Fab.)

A rather large, black flea beetle, with a red head, *Systena frontalis* (of the family Chrysomelidae), may be found more or less abundant in bean fields in New York every year. In dry seasons it is often numerous enough to cause considerable damage to the foliage (figs. 93 and 94). This insect has been found at Perry, New York, each year since 1917, and in 1918, when there was little rain, many beans turned yellow as a result of the feeding of this species and the closely related form, *S. taeniata*. Thirty beetles have been counted feeding on the upper surface of the leaves of a single plant. They often congregate on a few plants, seriously damaging them, while other plants are almost free from the pests.

S. frontalis is a common insect in the United States east of the Rocky Mountains, and in parts of Canada. It has been reported as injurious to grapes, cabbage, beets, potatoes, corn, beans, clover, cranberries, gooseberries, mangle-wurzels, and pear leaves. It is known to occur also on

FIG. 94. BEAN AND CLOVER LEAVES INJURED BY THE RED-HEADED FLEA-BEETLE

Japanese honeysuckle, weigela, aster, chrysanthemum, marsh mallow, rose mallow, smartweed, pigweed, lamb's-quarters, and ragweed. In addition to these hosts, the writer has found the species on goldenrod, daisy, broad-leafed plantain (*Plantago major* L.), black bindweed (*Polygonum convolvulus* L.), common burdock (*Arctium minus* Bernh.), heal-all (*Prunella vulgaris* L.), lady's-thumb (*Polygonum Persicaria* L.), wild lettuce (*Lactuca canadensis* L.), and beggar-ticks (*Bidens frondosa* L.).

Where *S. frontalis* has been found in large numbers, some of its weed hosts also have been abundant. Ragweed, lamb's-quarters, and beggar-ticks seem to be the most preferred.

DESCRIPTION OF STAGES

The egg

The egg of *Systena frontalis* is elliptical, slightly more rounded at one end, and is pale yellow in color (Plate LXXI, 6). The surface is roughened. Under high power these roughened areas are seen to be irregular, and they are made by the union of shallow grooves which form the borders of differently shaped polygons. The length is from 0.75 to 0.85 millimeter.

The larva

The larva (Plate LXIX, 7) is dirty white in color, appearing darker where the contents of the alimentary canal show thru the body. The largest diameter is at a point about two-thirds of the distance to the caudal end. The head is pale yellow, with darker markings on the lateral aspect near the lower side. The body is much wrinkled and is covered with many setae. On the caudal end there is a prominent erect tubercle bearing two pairs of prominent spines, and on the apex a tuft of fine hairs. An anal proleg is present. This description is from one specimen, 5.5 millimeters in length and probably nearly mature.

The adult

The adult (Plate LXXI, 8) is described by Blatchley (1910) as follows:

Resembles *hudsonius* very closely. Usually a little broader and less shining, the head reddish or reddish-yellow; antennae and legs mostly pale. Thorax more distinctly and elytra less coarsely punctate. Males in both species with the last ventral segment notched each side, the middle lobe with a deeply impressed triangular median line. Length 3.5–4.5 mm.

LIFE HISTORY AND HABITS

The egg

Immature eggs of *Systena frontalis* were found in dissected females on July 15, 1919. A few mature eggs were found in insects opened on August 5, and many were found in those dissected on August 18. From this time until September 15, eggs were found in beetles that were opened. Eggs deposited in the cages were found after August 6. In 1920 the insects were much later in appearing. The first beetles were taken on July 29, and specimens containing mature eggs were scarce until September 3. Most of the oviposition in the cages occurred early in September. It may be said, then, that the oviposition period varies greatly from year to year, occurring at any time in August or September.

After finding eggs in the laboratory cages, the writer searched for them in the field, and on September 20, 1919, a few were found around ragweed and lady's-thumb. After that date, eggs were frequently found on the soil near ragweed, and on September 5 three eggs were located near beggarticks. On September 11, eggs were found near a bean plant in a field where ragweed was growing among the beans, and in the same field, on September 15, one egg was discovered near a plant of lamb's-quarters. As previously stated, the eggs of *S. frontalis* and those of *S. taeniata* are very similar, but the eggs of *frontalis* are larger and are usually deposited later in the season than those of *taeniata*. The eggs of *taeniata* hatch in the fall, while *frontalis* winters in the egg stage. The eggs just mentioned as having been found in the fall of 1919 did not hatch that fall.

Eggs of *frontalis* have been found, in the field, scattered irregularly about the roots of its host plants and from one-half to two inches deep

Most of the eggs found have been near ragweed and beggar-ticks, tho a few have been found near other hosts.

The eggs of *S. frontalis* that have been under observation have never hatched during the same year in which they were deposited. Eleven eggs deposited on August 24, 1919, hatched between May 20 and 26, 1920. These eggs were kept during the winter on moist dirt in a petri dish in a cool room. Eggs deposited during September, 1920, and kept in a warm office, had not hatched by February 20, 1921. It would seem, therefore, that the egg stage of this insect covers about nine months. Scammell (1917) says: "Egg laying begins in late July, with deposition just below the surface of the ground. Hatching takes place the following May."

The larva and the pupa

Little is known of the larval stage of *Systena frontalis*. Two larvae hatching on May 25, 1920, were reared until June 15. At that time the larger one had reached a length of 5.5 millimeters and was probably nearly full-grown. The writer did not succeed in rearing these larvae thru to pupae. The larval stage is probably passed in feeding on the roots of the insect's weed hosts, but there are no definite data on the larval and pupal parts of the life history. A pupa believed to be that of *frontalis* was found near beggar-ticks in June, 1920, but as it could not be reared the identity is uncertain.

The adult

The red-headed flea beetles have been taken in the field from early in July until the first of October. They are most abundant on beans in August. Beetles have frequently been seen in copulation during August, and in 1920 some were observed as late as September 15.

Blatchley (1910) found the parent beetles of *Systena frontalis* wintering beneath the bark of white maple and in mullein, in Indiana. The writer has not succeeded in keeping the caged beetles alive thru the winter in New York, and, since this insect has not been found in the spring before July, it is doubtful that it hibernates as an adult in this State.

Red-headed flea beetles caged with ragweed or beans will feed actively for a few days and then go into the ground to deposit their eggs. In the field the same condition is found. After feeding on beans they move to ragweed, beggar-ticks, or some other host, where they may be found in numbers until they go into the soil for oviposition.

SEASONAL HISTORY

The parent beetle of *Systena frontalis* comes from the ground in July and August, and, after feeding on its cultivated and weed hosts, [illegible] ers the ground for oviposition during August and September. The [illegible] es over-winter near the plants, and hatch in May of the following year. [illegible] larval

and pupal stages are little known, but the larvae probably feed on the roots of ragweed, beggar-ticks, and other weeds, pupating sometime in June.

CONTROL

It has been pointed out that clean cultivation is an important factor in the control of *Systena taeniata*, and this is equally true for *S. frontalis*. The removal of ragweed, lamb's-quarters, and beggar-ticks from a field

FIG 95. SPRAYING MACHINE USED IN EXPERIMENTS FOR THE CONTROL OF FLEA BEETLES ON BEANS

after the eggs have been deposited in the fall and again before they hatch in the spring, should destroy many of the pests. Many of the insects breed along the edges of fields and in overgrown fence corners, and therefore keeping the weeds cleaned up in these places is a great help in reducing the number of beetles that may emerge.

In the summer of 1919, red-headed flea beetles were numerous in a bean field just across the road from the Perry laboratory, and control experiments were conducted there. On July 18, bean plants were sprayed with arsenate of lead (3 pounds of paste to 50 gallons of water), and twenty-five beetles were placed in a cage over these plants. The same number of

TABLE 12.—Control Measures Tested against Systena frontalis on Beans in 1919

Row	Material and method of application	Date of application	Length of row examined on July 17 (yards)	Number of *S. frontalis* present on July 17		Length of row examined on July 19 (yards)	Number of beetles present on July 19			
				Total number	Number per yard		*S. frontalis*	*S. bivittata*	Total number	Number per yard
26	Check		35	74	2.11	23	37	6	43	1.89
28	Lime—1 pound to 2 gallons water—compressed air sprayer	July 16	74	14	0.18	74	32	1	33	0.44
29	Check		35	37	1.03	26	18	8	56	2.15
31	Fish oil soap—½ pound to 2 gallons of water—compressed air sprayer	July 16	133	16	0.12	133	59	10	69	0.52
32	Check		37	70	1.89	133	131	14	145	1.09
34	Sulfur—1 pound to 2 gallons of water—compressed air sprayer	July 16	88	8	0.09	84	35	3	38	0.45
35	Check		40	67	1.45	26	36	7	43	1.65
37	Arsenate of lead paste—1:50—compressed air sprayer	July 16	60	5	0.08	55	8	0	8	0.14
38	Check		40	66	1.65	40	24	5	29	0.65
39	Bordeaux—5:5:50—arsenate of lead 1:50—barrel pump on wagon	July 14	90	6	0.06	288	17	1	18	0.06
40	Same as on row 39	July 14				288	21	4	25	0.08
44	Check		79	96	1.21	23	15	4	19	0.82
46	Arsenate of lead paste—1:50—barrel pump on wagon	July 17				84	6	2	8	0.09
47	Same as on row 46	July 17				84	5	1	6	0.07
48	Check					84	24	2	26	0.76
50	Land plaster dusted on plants	July 18				66	56	15	71	1.07
51	Check					25	31	13	44	1.76
53	Lime dusted on plants	July 18				54	25	12	37	0.68
55	Check					24	24	13	37	1.76
56	Basic phosphate dusted on plants	July 18				34	16	6	22	0.64
57	Check					20	21	4	25	1.25
59	Low ground bone dusted on plants	July 18				26	9	4	13	0.50
61	Check					18	12	10	22	0.78
62	[illegible]	July 18				30	13	15	28	0.93
63	[illegible]					28	18	6	24	0.85
[illegible]	[illegible]	July 18				21	10	1	11	0.17
[illegible]	[illegible]	July 18				41	27	3	26	0.63
						62	15	4	19	0.30

Average [illegible] beetles per yard

beetles caged over unsprayed beans served as a check. On July 24, eighteen of the twenty-five beetles were alive in the check cage but no live beetles could be found in the cage where arsenate of lead had been applied. Field experiments tested on a larger scale are listed in table 12.

For the experiments recorded in table 12, 94 rows of beans were planted in the field, running from east to west. At least one check row was left alternating with the treated rows. A compressed-air sprayer was used in some of the experiments, but in treating rows 39, 40, 46, and 47, a hand pump on a wagon (fig. 95), with a spray boom feeding twelve nozzles and covering four rows, was used. It was impossible to keep up sufficient pressure to feed all of the nozzles with this pump, and so the outfit would be unfit for practical work unless the boom was attached to a power sprayer or to an efficient traction machine. The three nozzles to a row covered both the upper and lower surfaces of the bean leaves. At this time the plants were still very small, but it is quite possible to spray beans when the vines are more developed. A small hand machine operated by a crank was used in applying the dusts.

Of the materials tested, the bordeaux-arsenate-of-lead spray gave the best results, but arsenate of lead alone was nearly as effective. It is apparent that arsenate of lead has good repellent qualities in addition to its killing power. Sprays of limewater, sulfur, and fish-oil soap also repelled the beetles, tho to a less extent; and several of the fertilizers dusted on the plants kept off some of the insects.

If beans become heavily infested with flea beetles in July, when the plants are small, and if growth is slow because of dry weather, spraying with the bordeaux-arsenate-of-lead mixture or with arsenate of lead alone is beneficial. If suitable machinery is not available for spraying, the plants may be dusted with lime or with a combination of arsenate of lead and lime. In all cases the wild hosts should be removed from fence corners, from the sides of the field, and from the field itself, soon after oviposition is finished in September.

THE GREEN CLOVER WORM

(*Plathypena scabra* Fab.)

During July and until October of 1919, the green clover worm (*Plathypena scabra* (Lepidoptera, Noctuidae) was very common on field beans in New York. The larvae of this snout moth may be found in small numbers on beans in almost any year, but only occasionally is it a serious pest. In 1917 and 1918 the writer found only four larvae of this species on beans.

Among the many hosts of the green clover worm are beans, lima beans, soybeans, peas, cowpeas, vetch, clover, alfalfa, strawberry, blackberry, tickweed, ragweed, smartweed, and wild carrot. The larvae that have been found on field beans in New York apparently belong to the second

generation. As the early-season hosts were not seriously injured, the first generation no doubt developed unnoticed and the pest appeared on beans in midsummer greatly augmented in numbers.

The green clover worm usually hibernates as a moth (fig. 96, B). In the fall the parent insect crawls into strawstacks, into barns, under the bark of

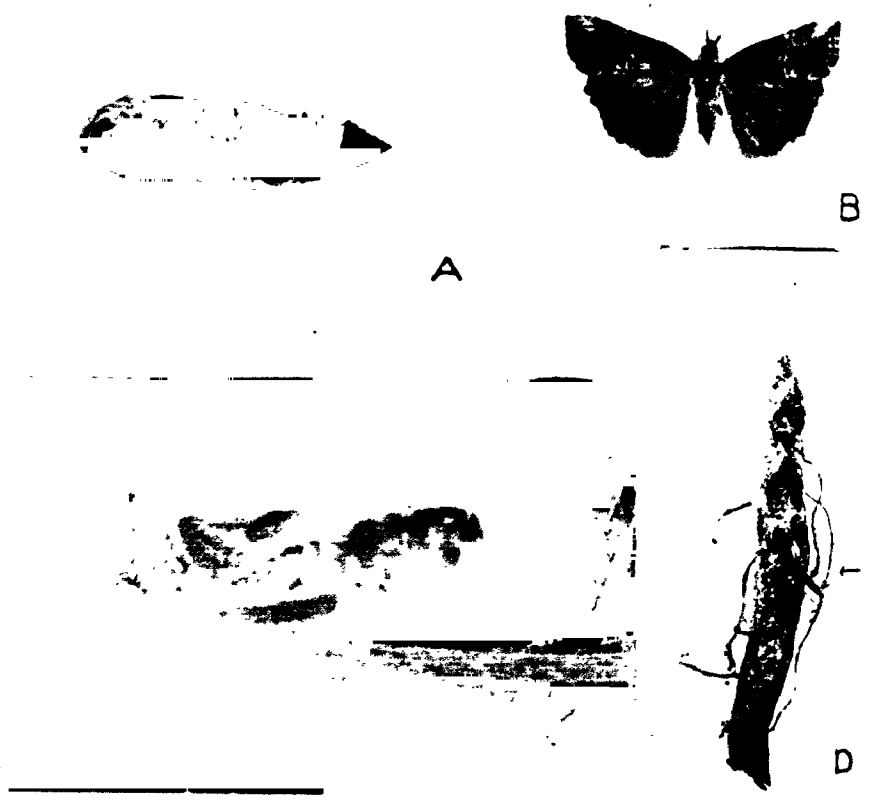

FIG. 96. PLATHYPENA SCABRA AND AGRIOTES MANCUS

A Pupa of *Plathypena scabra* ♂ about 3. B, Female moth of *P. scabra* slightly enlarged. C, Larva of *P. scabra* parasitized by larvae of *Rhyssalus lineatorius*, enlarged.
D, A larva of *Agriotes mancus* entering a diseased bean root, slightly reduced.

trees, or to any place where it may be protected from the cold. It is probable that under normal winter conditions a large proportion of these moths die before spring, but the winter of 1918–19 was so mild that the number of insects emerging from hibernation the following spring was far above the average. The mean temperature at Ithaca for the months of December, 1918, and January and February, 1919, averaged 11 degrees higher than

for the corresponding months of 1919–20. In the summer of 1920, which followed an unusually severe winter, the writer could find only one larva of this pest. This was a parasitized specimen (fig. 96, C) found on June 3 on clover, from which eight specimens of *Rhyssalus loxoteniae* Ashm.[8] were reared. From a larva taken on beans on August 22, 1919, another parasite, *Aleiodes intermedius* Cress.,[8] emerged on September 4.

When undisturbed, the larva of *Plathypena scabra* rests quietly on the leaf and is inconspicuous by reason of its pale green color (fig. 97, B); but when the plant is shaken, the larva may drop to the ground and squirm back and forth for some time, or it may remain suspended in mid-air by a fine silken thread. The older larvae are voracious feeders. They eat entirely thru a leaf (fig. 97, A), and sometimes make large holes in the pods (Plate LXX, 5).

The pupa (fig. 96, A) is mahogany

FIG. 97. WORK OF THE GREEN CLOVER WORM

A, Bean leaves injured by feeding of the worm, reduced. B, Larva feeding on a bean leaf, slightly enlarged.

[8] Determined by C. F. W. Muesebeck.

brown in color, is about 12 millimeters in length, and bears several hook-like spines on the end. This stage of the insect is usually passed above or below ground in a frail cocoon covered with particles of dirt.

The moths of *P. scabra*, reared from larvae found on beans at Perry in July, emerged in cages from August 25 to October 1. Late in September there were many moths in the fields around the piles of drying beans. No eggs were deposited by moths in cages before they were killed by cold weather.

The larvae found in a field at any one time vary greatly in size, and some larvae could still be found when moths were seeking hibernating places. On September 9 larvae of all sizes were taken on beans, and more were found on ragweed on October 2. It seems probable that there are normally two broods of this insect in New York, but that in long warm summers there may be a partial third brood.

When the larvae of *P. scabra* appear in such large numbers that they threaten the bean crop, they may be controlled by a spray of arsenate of lead, 2 to 3 pounds of paste to 50 gallons of water. To insure the destruction of all larvae, the under as well as the upper sides of the leaves should be covered. Sherman and Leiby (1920) found that the pest could be controlled when feeding on soybeans by dusting the plants with a combination of 1 part of powdered arsenate of lead to 8 parts of lime. The material must be applied as soon as the insects begin their work. A hand duster, geared to distribute two pounds to the acre, is recommended by these writers.

On wax and string beans it is not always safe to apply a poison to the pods. To kill the insects on plants of this type, a spray of Black-leaf-40 (1 gallon to 750 gallons of water), with the addition of soap (3 pounds to 50 gallons of water), should be used. For small gardens, a mixture of one teaspoonful of Black-leaf-40 and one ounce of laundry soap in one gallon of water has been found effective. As the larva is killed only when thoroly drenched by the spray, it is necessary to cover both the upper and the under sides of the leaves.

THE BEAN WEEVIL

(*Acanthoscelides* [*Bruchus*] *obtectus* Say)

There is no other bean pest as well known and as much discussed in entomological literature as the bean weevil, *Acanthoscelides obtectus* (Coleoptera, Bruchidae) (fig. 98). It is not a field pest in New York, but, since it frequently causes great loss to beans in storage, a brief discussion of it may be justified in this paper.

When beans that have been infested in the field are kept in a warm storeroom, the reproduction of the weevil continues, and generation after generation develops in the stored seed. The same thing may happen when uninfested beans are put in a warm place where the weevils are already

present. This work in stored beans is the only loss occasioned by this insect in New York (Plate LXXI, 3).

In an effort to determine the summer habits of the weevils that emerge from infested seed when it is planted, the writer, on June 18, 1918, placed weevils, and beans containing larvae and pupae of the insect, in a field cage in which small bean plants were growing. On July 2 it was noted that the parent beetles had eaten small pieces from the leaves of the plants; and on August 15 the beans just below the surface of the ground, that had not germinated, were filled with larvae, pupae, and adults of the insect. This condition still prevailed on October 1.

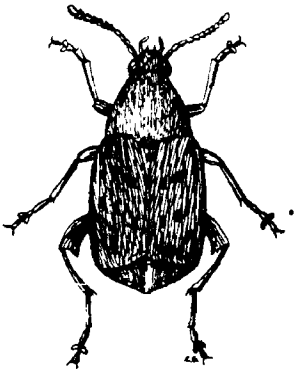

FIG. 98. THE BEAN WEEVIL, ACANTHOSCELIDES OBTECTUS

Bean weevils are not a serious pest under New York conditions, because of the low temperature during the winter. Garman (1917) has shown by experiments that a temperature of 0° F. for twenty-four hours will destroy all stages of this pest. Thus the insects are probably never able to live thru the cold winters in the bean fields. At a temperature of 50° F., feeding and reproduction are so checked that little harm results. A grower in New York who saves his seed from his crop of the preceding year and keeps it in a barn or some other cold place, need have little fear of weevil injury. The same is true where seed is kept in bean warehouses at low temperatures. In warm stores and seedhouses, however, which often have a few weevils present in left-over stock, the continuous multiplication of the pests often results in almost total destruction of the beans.

FIG. 99. THE BLUE-BANDED MILLEPEDE, × 2½

THE BLUE-BANDED MILLEPEDE
(*Julus caeruleocinctus* Wood)

In July, 1917, a bean field near Batavia, New York, showed a heavy infestation of the millepede, or thousand-legged worm, *Julus caeruleocinctus* (of the order Diplopoda) (fig. 99). The soil in this field is sandy, and when observed by the writer it was dried out and crusted, altho only two weeks before it had been very wet. The millepedes were feeding on the plant parts below ground and had eaten the main roots to such an extent that some of the plants were almost severed from them (fig. 100, C). Nearly every plant

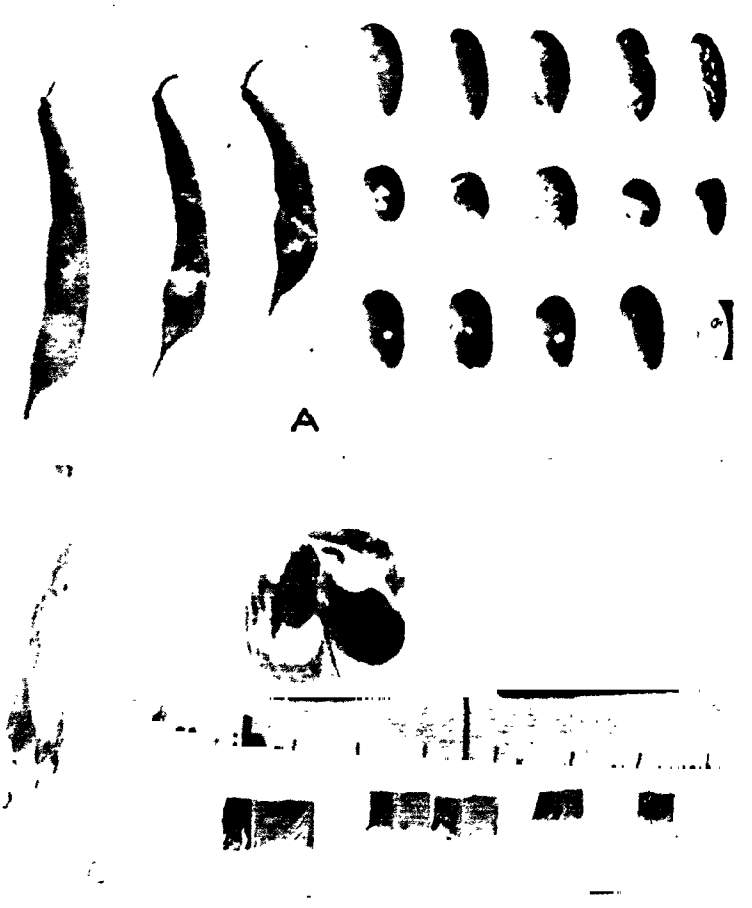

FIG. 100 SOME INJURIES TO BEANS

A, Bean pods punctured many times by *Aphis rapidus*, reduced. B, Dimpled [illegible] caused by punctures of sucking insects and bottom row by a No. 2 insect pin with which [illegible] were pricked while still in the pod. C, Cavities made by the feeding of *Tylus caeruleocinctus* [illegible]. D, insect cages used in experiments in the transmission of bean blight.

had been attacked, and frequently there were from five to ten of the pests around a single seedling. Reports of similar injury to beans were received from Orleans and Allegany counties.

J. caeruleocinctus shows a preference for decaying vegetable matter when this is present, but tender growing plants of fleshy texture [illegible] be eaten. In Lintner's early writings, records may be found of injury to [illegible] cantaloupes.

melons, radishes, potatoes, and turnips. Lintner cites also an instance of injury to nursery stock which was planted after an infested crop of potatoes. The writer has observed these millepedes feeding beneath the ground on young hop vines before they had become hardened, and they have often been found in decaying roots and vines that had been injured by the hop-vine borer (*Gortyna immanis* Guenée). Millepedes thrive under moist conditions, and their attraction to growing plants is often due to decay started in the tissues by excess moisture.

The blue-banded millepede is said to deposit its small, white, spherical eggs in the spring, in clusters surrounded by particles of dirt and excreta. In midsummer, specimens of all sizes may be found feeding together. Two hundred millepedes were found in one potato by Lintner. The pests often gather and crawl over one another, forming moving balls of animal life. Late one evening in September, 1919, at Perry, hundreds were found crawling on sidewalks, in gutters, and even up the sides of houses. By morning they had nearly all disappeared.

There is no satisfactory control for millepedes under field conditions. A bait of poisoned potato buried in the ground is said to be of use in gardens. Tobacco dust seems to have some repellent effect, and on a small scale spraying the ground with Black-leaf-40, 1 part to 750 parts of water as recommended for control of the hothouse millepede (*Oxidus gracilis* Koch), may be effective.

THE SOLANUM ROOT LOUSE

(*Trifidaphis radicicola* Essig[1])

Each year a few bean plants have been found with their roots serving as hosts for the solanum root louse, *Trifidaphis radicicola* (Homoptera, Aphididae). If the aphides are numerous, the leaves turn yellow and the plants take on a wilted appearance, due to the injury to the lateral roots caused by the feeding of the pest. Infested plants have been found from June 22 to August 22. Only the apterous forms of the insect were seen, and usually there were more immature than fully developed lice present. These aphides are cream-colored, but their powdery covering frequently gives them a white, woolly appearance. An ant, *Solenopsis molesta* Say, is often in attendance.

A bean grower near Castile, New York, informed the writer that in 1915 his entire field was so badly attacked that the crop was ruined. When beans were planted in this field the next year they were again infested and had to be dragged up. Lice of this species have also been found in small numbers near Batavia, in Genesee County.

T. radicicola is reported from California by Essig (1909 and 1913) as feeding on rough pigweed (*Amaranthus retroflexus*), beet (*Beta vulgaris*), black nightshade (*Solanum nigrum*), and potato (*Solanum tuberosum*).

[1] Determined by Miss E. Patch.

It is probable that the insect may be found on weeds in New York and is injurious to beans only when they are planted after other infested hosts.

THE WHEAT WIREWORM
(*Agriotes mancus* Say)

Larvae of the wheat wireworm, *Agriotes mancus* (Coleoptera, Elateridae), may be found each year feeding in the roots of field beans near Perry, New York (Plate LXX, 4). This is especially noticeable when the plants are already weakened by the dry root-rot caused by *Fusarium martii phaseoli*. The taproot, partly destroyed by the disease, is a place of easy entrance for the larvae (fig. 96, D, page 1012), and when once inside they frequently eat their way upward as far as the first leaves. Several specimens may be found in a single plant, and if the root-rot also is present the plants often have a drooping, wilted appearance. It is usually impossible to absolutely distinguish the injury caused by the insect from that caused by the disease. Rarely have plants with healthy roots been found to contain wireworms.

Larvae of this species have also been found feeding in the roots of Lamb's-quarters and of ragweed growing in bean fields. The life history of the insect covers a period of three years (Hyslop, 1916). Adults were taken by sweeping during May and June in 1919.

As far as the writer has observed, serious injury from wireworms has been restricted to single plants, or, at most, to small parts of a field, and their presence may be explained by the practice of planting beans after sod, which is the normal host of the insect.

THE RED SPIDER
(*Tetranychus telarius* L.)

In a summer that is hot and dry, beans may suffer from the red spider, *Tetranychus telarius* (of the order Acarina) (Plate LXXI, 5). In 1918 the plants on the experimental field at Perry were covered with these pests, the leaves turned yellow and the growth was stunted. The total rainfall at Perry during July and August of that year was only 2.37 inches, whereas the normal for these two months is 6.05 inches. In 1919 the red spider was common in some parts of Genesee, Orleans, and Niagara Counties, where again the rainfall was below normal. It may be occasionally found on beans in any year, but when the growth of leaves is luxuriant the slight damage that it causes is easily overlooked. This mite has many native hosts, and fields that have weeds along the edges or between the rows usually show a heavier infestation.

Injury by *T. telarius* may be recognized by many small brown spots on the upper surface of the leaves, where the plant cells are killed. On the under surface of the leaves, small webs may be observed, and the small yellow, green, or red mites may be found crawling or feeding among

the strands of silk. Each brown area seen on a leaf represents the place of feeding of a mite below, and as these marks increase, the leaf becomes spotted, turns a sickly yellow, and in some cases drops. The lower leaves are attacked first, and as these are destroyed, the small creatures climb higher in search of new food.

WHITE GRUBS, OR MAY BEETLES
(*Phyllophaga* sp.)

White grubs, the larvae of May beetles (Coleoptera, Scarabaeidae), tho occasionally found, have not been reported as a serious pest of field beans in western New York during the past four years. In 1917 the beetles were present in very large numbers around electric lights at Perry. The writer had 184 specimens, collected between June 12 and June 25, identified by Mr. Henry Dietrich, who found 137 *Phyllophaga fusca* Froh. males and 38 *fusca* females, and 6 *P. anxia* (*dubia*) Leconte males and 3 *anxia* females. *P. fusca* is believed by Forbes (1916) to pass thru a three-years cycle. In 1920 a few beetles were collected around lights, but this brood was much smaller than the one observed in 1917. In rare cases the writer has found, in digging around a wilted bean plant, that a white grub had cut it off. Several plants of this type were found in 1919, and one beetle (*fusca*), bred from a grub found on July 3, changed to the adult stage on September 1. It would have emerged normally in the spring of 1920.

Injury from white grubs occurs usually when cultivated crops are planted after sod in a year following one in which there was a large emergence of parent beetles. The May beetles, according to Davis (1918), prefer to oviposit in fields of oats, barley, wheat, timothy, or sod, rather than in those where there are good catches of clover and alfalfa or where there are cultivated crops such as corn and beans. In western New York a common rotation is one of wheat, clover, and beans. If, in this New York rotation, the beetles are abundant during the year when a field is in wheat, there may be many small larvae present the next year; but, since the grubs do not seriously damage clover, the crop then growing, they might easily escape notice. As neither clover nor beans are attractive to the beetle for oviposition, it is evident that when this rotation is followed, little damage from the grubs should be experienced in western New York. Serious infestations of the grub occur only when pasture land or a crop of one of the small grains, such as barley, oats, or wheat, is followed the next year by beans.

THE ROSE CHAFER
(*Macrodactylus subspinosus* Fab.)

In the summer of 1917, beans in many parts of New York were damaged by the rose chafer, *Macrodactylus subspinosus* (Coleoptera, Scarabaeidae),

Reports of injury to the bean crop by this insect were received from Fulton, Lewis, Madison, Essex, and Warren Counties. The principal injury results from the active feeding of the long-legged, grayish brown, adult beetles, which have been reported as destroying as much as 40 per cent of the leaves. Injury from this pest in 1917 was reported between June 28 and August 2.

On grapes, a spray of arsenate of lead (4 pounds of paste to 50 gallons of water or bordeaux mixture, with the addition of 2 gallons of cheap molasses) is said to be the most effective method of control. This should control the insect on beans also. The spray must be applied thoroly as soon as the first beetles are seen, and repeated if rains wash off the first application. Every leaf should be covered, and as a new growth develops this also should be coated with the spray.

THE SOUTHERN CORN ROOTWORM
(*Diabrotica duodecimpunctata* Fab.)

The small, yellowish green beetle (Plate LXXI, 7) known in the South as the southern corn rootworm, *Diabrotica duodecimpunctata* (Coleoptera, Chrysomelidae), and sometimes called the twelve-spotted asparagus beetle, is occasionally present in small numbers on beans in New York. In 1917 it was reported to be causing some injury to the leaves. The parent insect is a general feeder and may be found on many cultivated crops as well as on weeds that occur in and around fields and gardens.

In the South the larvae feed underground on corn and cause immense losses by killing the developing bud. The insects have been found attacking the roots of beans in New York, but there have been so few of them present that the damage to this crop has been negligible. The feeding of the parent beetle on the foliage may be controlled by a spray of arsenate of lead, 2 pounds of paste to 50 gallons of water.

THE BEAN LEAF BEETLE
(*Cerotoma trifurcata* Forster)

Each year a few specimens of the bean leaf beetle, *Cerotoma trifurcata* (Coleoptera, Chrysomelidae), have been found on beans in western New York, but they have not been present in sufficient numbers to cause appreciable damage. The parent beetle (Plate LXXI, 9) is about one-third of an inch in length, and is yellowish in color, with a black head and black markings on the wing covers.

The bean leaf beetle has been found on beans from July until the middle of September. It has been noticed also on ragweed and lamb's-quarters growing in bean fields, and on carrot tops near by. Bush clover, hog peanuts, and beggarweed are likewise reported as hosts. At rare intervals the insect appears in parts of this and other States, destroying field and garden beans, soybeans, and cowpeas by feeding on the leaves.

When control measures are necessary, a spray of arsenate of lead, 2 pounds of paste to 50 gallons of water, applied when the beetles first appear, will suffice.

THE APPLE LEAF HOPPER
(*Empoasca mali* LeB.[19])

The apple leaf hopper, *Empoasca mali* (Hemiptera, Cicadellidae (Plate LXXI, 4), has at times been found in small numbers on field beans at Perry, but the insects have not been connected with any deformation of the plant. In some parts of the State, particularly near Lake Ontario, where pea beans are grown, this insect has been more plentiful, and it has seemed probable that bean mosaic, a destructive disease of pea beans, may be transmitted by this pest. This disease, however, which may be recognized by a curling of the leaves and the appearance of mottled light-and-dark areas on the foliage, has been known to occur and spread when leaf hoppers were not present.

Dr. Robert Matheson, working in conjunction with Dr. Donald Reddick, of the Department of Botany at Cornell University, found that he could produce a curling of the leaves of pea bean plants when leaf hoppers transferred from infested beans were caged over healthy plants. These plants later outgrew the curling, however, and mosaic did not develop, and so the experimental evidence would tend to show that the disease is not carried by *E. mali*. Further tests must be made before a definite statement can be given.

GRASSHOPPERS
(*Melanoplus atlantis* Riley, M. *femur-rubrum* DeGeer, and *M. bivittatus* Say)

Bean fields with a border of grass and weeds, or adjoining meadows or pastures, are often attacked by grasshoppers. Nearly every year a few poorly-cared-for fields have shown some injury. Three specimens of grasshoppers have been mainly blamable for the work — *Melanoplus atlantis*, *M. femur-rubrum*, and *M. bivittatus* (Orthoptera, Acrididae). The eggs of the insects have often been found in fence corners or in the sod border of fields, and many newly hatched nymphs have been taken in these places during May and June. The beans near the edges of fields usually suffer the most; in fact, it is not unusual to find the plants of the first few rows riddled by the pests, while the central part of the field is unharmed.

INJURIES TO BEANS IN THE POD, CAUSED BY HEMIPTEROUS INSECTS
(*Adelphocorus rapidus* Say, *Euschistus variolarius* Palisot de Beauvois, *Lygus pratensis* L.)

During the past four years the Cornell University Agricultural Experiment Station has received many samples of beans showing deformations

[19] Determined by E. D. Ball.

which varied from circular depressed areas, each with a dark spot in the center, to ragged holes, with the bean coat badly ruptured (Plate LXXI, 2, and fig. 100, B). The term *dimples* has been applied to these scars.

Since these markings bear a strong resemblance to hemipterous punctures on other plants, specimens of the dusky plant bug, *Adelphocoris rapidus* (fig. 101), one of the commonest mirids in western New York bean fields, were caged over a potted bean plant on August 15, 1918. When examined on September 4, the pods on this plant were misshapen and covered with dark, raised, wart-like areas (fig. 100, A). The seed in these pods showed evidence of dimpling.

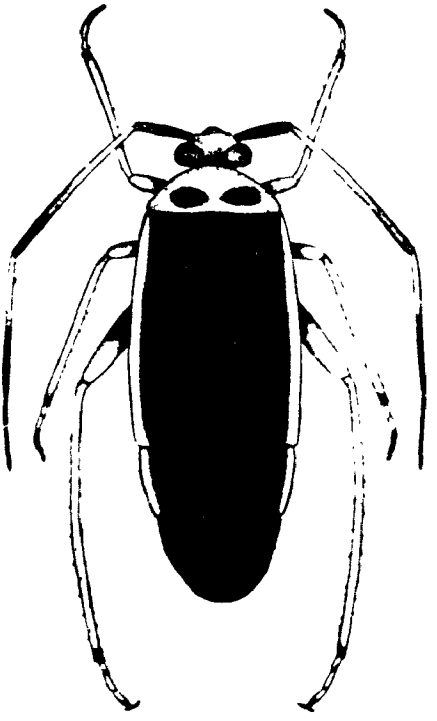

FIG. 101 THE DUSKY PLANT BUG, ADELPHOCORUS RAPIDUS

Reproduced by courtesy of the Iowa College Agricultural Experiment Station

In the summer of 1919 an effort was made to verify this observation and to find other insects that might have a share in the work. On August 11 a cage containing *A. rapidus* was placed over two bean plants, the pods of which were still green. When these were examined on August 28, most of the beans were dimpled. One hundred pods picked near the cage contained only one dimpled seed.

The feeding of *A. rapidus* frequently produces such ragged, discolored marks on the bean seed that it would seem that the insect, in addition to removing juices from the bean, possibly secretes a toxin that acts on the bean tissues. The nature of the puncture appears to be influenced by the stage of development of the pod at the time of the attack. The seed is stunted when punctured, and the subsequent growth about the injured part produces the dimple. Beans the pods of which are still green tho nearly mature, to feel to suffer the most. In addition to feeding on the pods, the insect attacks also the blossoms, the leaves, and the stalks, but on these no serious deformation seems to result.

It is not always easy to distinguish, by their outward appearance, the pods that contain dimpled beans. The pods may be free from the roughened brown areas and still contain injured beans. Some have been found

on which only a dark green spot on the lighter green of the pod gave evidence of the deformation within.

Other insects that produce pits in beans are the spined tobacco bug (*Euschistus variolarius*, Plate LXXI, 1), of the family Pentatomidae, and the tarnished plant bug (*Lygus pratensis*). Specimens of *Euschistus variolarius* placed with beans on August 19 had produced small pits on them by September 8. Nymphs and adults of *Lygus pratensis* left with a plant for nineteen days also produced small dimples. Similar work of this insect was reported from Michigan some years ago. During late summer both these insects, together with the apple leaf hopper (*Empoasca mali*), have been found in the field with their beaks inserted in the pods. Cage experiments seem to show, however, that the beak of the leaf hopper is too short to penetrate the pod and injure the beans within. In the summer of 1920, these experiments were repeated and the injuries from the insects were of the same kind as had been caused by them the preceding year.

The extent of the damage caused by these pests is not great, but each year there are a few beans of this kind in the product of almost all fields and gardens. Injury is especially noticeable in places where ragweed and lamb's-quarters are allowed to grow. The most disfigured of the field beans are discarded, with the diseased and immature seed, when they are picked and graded in the warehouse.

THE RÔLE OF INSECTS IN THE TRANSMISSION OF BEAN DISEASES

Bean diseases frequently spread thru a field with great rapidity, and it sometimes appears as tho this spread might be due to, or at least hastened by, the presence of insects. In cooperation with Dr. W. H. Burkholder, of the Department of Plant Pathology at Cornell University, experiments were conducted in the summer of 1918 in an effort to determine what insects were instrumental in the spread of the bacterial blight of beans (caused by *Bacterium phaseoli* E. F. Smith).

On August 22, 1918, eight specimens of each of the commoner insects on bean foliage, including the red-headed flea beetle (*Systena frontalis*), the dusky plant bug (*Adelphocoris rapidus*), the apple leaf hopper (*Empoasca mali*), and the nine-spotted lady bug (*Coccinella novemnotata*), were rubbed in a virulent culture of the blight organism or allowed to crawl for an hour on bean leaves smeared with the culture. The insects were then placed in separate field cages (fig. 100, D, page 1016) on varieties of beans free from blight but susceptible to it. As a check, insects of the same species, collected in the same field but not treated with the pathogene, were placed in similar cages. Blight did not develop in any of the cages.

In 1919 the same species of insects that were used in 1918, and in addition the tarnished plant bug (*Lygus pratensis*), were used in the experiments. The insects were taken from a severely blighted field of red kidney beans, and after being caged for some time with these diseased plants they were

placed in field cages with beans free from the disease. Blight did not appear in any of the cages.

In examining bean seed punctured by *Adelphocoris rapidus*, Dr. Burkholder has found undetermined bacteria present in large numbers. It would seem, therefore, that this common sucking insect might be capable of transmitting the organism that causes bean blight, but most of the evidence thus far obtained is negative.

It is unusual to find *A. rapidus* present in sufficient numbers to be the sole agent in the spread of blight. The writer still feels that the commoner *Lygus pratensis* may sometimes carry the disease as it migrates from plant to plant in search of food, and further experiments should be carried on with *Empoasca mali* before it is safe to say that this species is not partially blamable for the spread of the blight organism. Plant lice have been found but rarely on beans in New York, and never in quantities that would justify placing much blame on them.

Dr. Robert Matheson, working in conjunction with Dr. Donald Reddick, of the Department of Botany at Cornell University, found that he could transfer bean mosaic, the causal organism of which has not been isolated, from one bean plant to another by means of an undetermined plant louse, but that *Empoasca mali*, *Lygus pratensis*, *Systena hudsonius*, *Systena frontalis*, *Epitrix cucumeris*, and *Tetranychus telarius*, seemed unable to transmit the disease.

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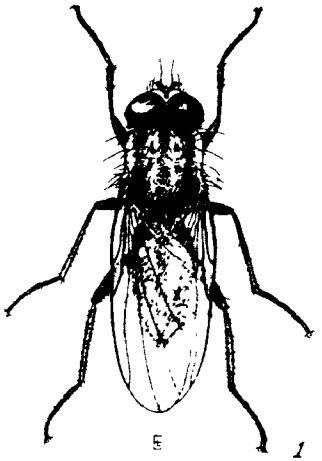
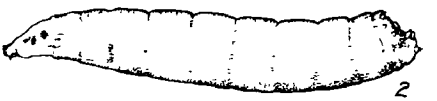
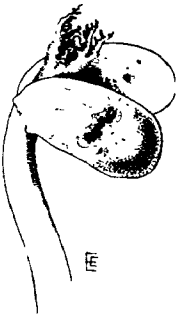
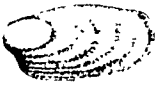
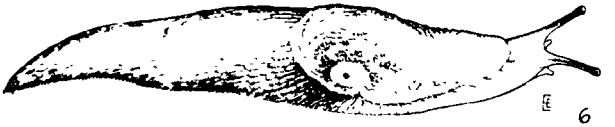
PLATE LXIX

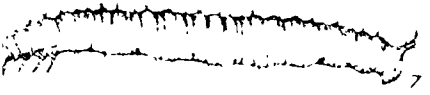


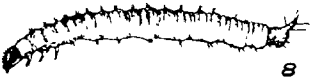


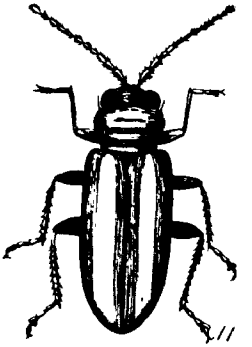












LEMA CILICRA, AGRIOLIMAX AGRESTIS, ARION CIRCUMSCRIPTUS, SYSTENA TAENIATA, AND SYSTENA FRONTALIS

Lema cilicrura 1, Parent fly, with wings in normal overlapping position, × 8. 2, Larva, or maggot, × 3. 3, Hind leg of male, showing the row of regular bristles on the tibia, × 18. 4, Injury to the plumule and cotyledons of a bean seedling, caused by the larva of *H. cilicrura*, × 1½.
Agriolimax agrestis 5, The shell. 6, The slug. 10, The jaw of *A. agrestis*. (All redrawn after Taylor)
Arion circumscriptus 12, A common imported slug, *Arion circumscriptus*, × 2.
Systena taeniata 8, The larva, × 9. 9, The pupa, × 9. 11, The adult beetle, × 8.
Systena frontalis 7, The larva, × 9.

JUNE, 1922 MEMOIR 56

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

THE INSECT FAUNA OF THE GENUS CRATAEGUS

WALTER H. WELLHOUSE

ITHACA, NEW YORK

PUBLISHED BY THE UNIVERSITY

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THE INSECT FAUNA OF THE GENUS CRATAEGUS

THE INSECT FAUNA OF THE GENUS CRATAEGUS

WALTER H. WELLHOUSE

This paper is submitted as a result of three years of study of the insects that feed on the plants belonging to the genus Crataegus. The writer's object at the time when the work was undertaken was primarily to learn, by collecting and rearing, what insects occur on the trees of this genus in central New York. As the interest in the work increased, it was decided to widen the field and make the list more complete by including the insects that other workers have found to be eaters of Crataegus.

There are three older lists of insects feeding on Crataegus which have been helpful in the preparation of the present catalog. Kaltenbach (1872)[1] gives a list of 104 European species, Packard (1890) gives 46 American species, and Felt (1906) gives 28 American species. With the exception of these three lists, the material included in this paper is gathered from widely scattered references and from the writer's observations. Since food-plant indices are very commonly omitted from entomological writings, it is difficult to get a list of all the insects that feed on a plant. Such a list can be obtained only by scanning the pages of a multitude of papers containing biological notes on all orders of insects. Much of that kind of work has been done in the preparation of this catalog, but, since it has not been possible to see all papers that might contain accounts of insects feeding on Crataegus, the writer does not claim that his list is complete.

The catalog contains 382 species, representing 9 orders and 55 families. They are distributed as follows:

Acarina, 10 species		Thysanoptera, 1 species:	
Eriophyidae	7	Thrypidae	1
Phyllocoptidae	1	Coleoptera, 74 species.	
Tetranychidae	2	Elateridae	3
Orthoptera, 4 species.		Buprestidae	6
Gryllidae	1	Scarabaeidae	4
Acrididae	3	Cerambycidae	5
Odonata, 1 species.		Chrysomelidae	12
Agrionidae	1	Curculionidae	40
Homoptera (including Homoptera?, 84 species.		Ipidae (Scolytidae).	2
		Anthribidae	1
Miridae (Capsidae)	12	Dermestidae	1
Tingitidae	4	Lepidoptera, 184 species:	
Membracidae	4	Papilionidae	2
Cicadellidae (Jassidae).	18	Nymphalidae	2
Psyllidae (Chermidae)	7	Pieridae	1
Aphididae	22	Lycaenidae	3
Coccidae	17	Sphingidae	3

[1] Dates in parenthesis refer to *Literature Cited*, page 1088.

Lepidoptera (*continued*):		Lepidoptera (*continued*):	
Saturnidae	3	Yponomeutidae	7
Arctidae	3	Gelechiidae	6
Noctuidae	27	Elachistidae	5
Notodontidae	6	Gracilariidae	12
Lymantriidae	7	Glyphipterygidae	2
Lasiocampidae	10	Nepticulidae	11
Geometridae	27	Cosmopterygidae	2
Drepanidae	1	Lyonetidae	4
Nolidae	1	Diptera, 16 species.	
Psychidae	1	Cecidomyiidae (Itonididae)	15
Limacodidae	1	Trypetidae	1
Cossidae	1	Hymenoptera, 8 species:	
Sesiidae (Aegeriidae	3	Tenthredinidae	7
Pyralidae	3	Chalcididae	1
Tortricidae	30		

The catalog includes insects that have been taken on the Crataegus trees in five continents. The number of species reported from each continent is as follows: North America, 213 species; Europe, 203; Asia, 88; Africa, 11; Australia, 8. All but 45 of the North American species are believed to be distinct from those of the Old World. A single Australian species is distinct from those of other continents. The insects recorded from Asia and Africa are found also in Europe.

It will be noticed that the mites, which have similar habits, are included with the insects in this paper.

Some helpful references to entomological notes concerning each species have been included in the catalog, which is intended as an aid to other workers who are investigating the insects of our deciduous fruit trees and related plants.

Grateful acknowledgment is made to Professors Glenn W. Herrick and James G. Needham, of the Department of Entomology at Cornell University, under whose direction the work was done and whose kindly criticisms and suggestions are appreciated, also to Dr. W. T. M. Forbes, Dr. Edith M. Patch, Chas. W. Leng, Dr. P. B. Lawson, Professor Z. P. Metcalf, Dr. H. H. Knight, Professor Carl J. Drake, Dr. E. P. Felt and Henry Dietrich, who have kindly aided in the determination of species; to Dr. K. M. Wiegand, who has kindly aided in the determination of species of Crataegus; and to Miss Lela G. Gross for able editorial assistance.

THE GENUS CRATAEGUS

Crataegus is the name of a group of trees and shrubs commonly known by their sharp thorns, white flowers (pink or red in a few cultivated varieties) in May, and red or yellowish fruit like miniature apples in autumn. It is an ancient Greek name derived from *kratos* (strength), and was applied to the plants of this genus because of the hardness and durability of the wood.

Among the popular names by which the genus is known most commonly are the following: hawthorn, thorn apple, red haw, white thorn, and thorn, in America; hawthorn and may, in England; aubepine, in France (snellier, by French Canadians); Weissdorn, in Germany; spinalba, in Italy. As the name *hawthorn* seems to be the one most commonly used by English-speaking peoples, the writer has used it in this paper to represent all species of Crataegus.

The genus is placed by many botanists in the family Rosaceae. Other botanists have divided the Rosaceae group and formed an apple family, Malaceae, in which Crataegus is included along with Malus, Pyrus, Cydonia, Mespilus, Sorbus, Amelanchier, Aronia, and Eriobotrya.

The determination of species of Crataegus is as great a taxonomic problem to botanists as the determination of the parasitic Hymenoptera is to entomologists. During the first ten years of this century about one thousand species of Crataegus were described in North America. Many of them are now regarded as hybrids and varieties, and a still further reduction of species is in progress. This taxonomic uncertainty makes it impossible in many cases to recognize specific hosts for the insects that feed on the hawthorns.

Crataegus is distributed over most of the temperate parts of the Northern Hemisphere. The genus is not indigenous in the Southern Hemisphere except in America, where it follows the unbroken mountain chain through the Tropics and grows in the Andes Mountains. It is found as far north as Newfoundland, Norway, and Sweden, and extends southward to the Mediterranean borders of Africa and Asia Minor. The European species have been introduced into Australia and other European colonies in the Southern Hemisphere for cultivation.

Most species of hawthorns seem to thrive in any well-drained soil which is not acid and where rainfall is sufficient for the growth of forest trees, while a few species thrive in acid soils also. They are usually long-lived trees and individuals one hundred years old are not uncommon.

Distribution is effected largely by means of birds and mammals, which eat the ripe fruits and carry the seeds in their digestive tracts to other communities. Within the same community, thickets are commonly formed from the new stems which grow from the roots of a single tree. Wherever the roots become exposed to light, as by washing on hillsides, a new stem may grow and a tree be formed from it.

ECOLOGICAL SUMMARY

The ecological relations of the hawthorns to their insect fauna may be summarized in a general way very briefly. The two basic needs of an insect which it is possible for a host plant to supply are food and shelter. The hawthorns furnish both food and shelter.

They furnish food for nearly all of the insects studied. A few exceptions, such as the snowy tree cricket (*Oecanthus nivens*) and the damsel fly *Lestes viridis*, procure their food elsewhere and use the hawthorn branches merely to shelter their eggs from the weather and their enemies. Every part of the tree furnishes food for some species of insect, as may be seen from the following outline:

Trunk and branches	40 species
A. External feeders (scales, aphids, and others), 19	
B. Internal feeders (borers), 21	
Roots (aphids)	1
Thorns (weevils)	1
Leaves	292
A. External feeders (miscellaneous), 235	
B. Miners (tineids, weevils, sawflies), 37	
C. Gall makers (aphids, mites, cecidomyids), 20	
Flowers (thrips, maggots, caterpillars, beetles, and others	12
Fruit (caterpillars, bugs, maggots, grubs	30

The other basic need of insects which a host plant may supply is shelter. Most of the insects included in this paper are sheltered to some extent by the hawthorn, although the completeness of the shelter varies with the habits of each species of insect. Some are protected only by their position on the surface of the tree. Others are partially sheltered in rolled leaves, bark crevices, and the like. Still others are securely housed within the plant tissues. The degree of shelter secured by those species living externally on the surface of the plant varies so greatly and so gradually that no distinct lines of division can be drawn in so general a statement as this. The more distinct groups of internal feeders (borers, leaf miners, and gall makers) are indicated above and are distinguished from the external feeders, which receive less complete shelter.

The fact that so many species of insects feed at the expense of the hawthorns suggests the idea that these trees are in danger of extinction. Such is not the case, however, for the hawthorns when not weakened by drought or flood are very hardy, long-lived trees. Some indications as to why they so successfully withstand the feeding of the insects may be seen from a study of the following data, which are based on statistics given in the last sections of this paper:

APPROXIMATE FEEDING PERIOD OF HAWTHORN INSECTS

	Species	
March	11	August
April	54	September
May	190	October
June	232	November
July	131	Time of feeding unknown

FOOD PLANTS OF HAWTHORN INSECTS

Food plants restricted to Crataegus	
Food plants including other related or associated groups	

It will be noticed that there is a direct correspondence between the time of feeding of the insects and the time of growth of the trees. The greatest number of species feed during May and June, when the trees make their greatest growth. The number decreases slightly during July and August, at the time when droughts frequently check tree growth, and then it increases slightly in September, at the time when fall rains often cause a new growth. This relationship between the period of growth and the time of feeding seems to be one of Nature's adjustments for maintaining balance.

The fact that a large majority of the insects feed on other host plants also, lessens the danger of destruction of the hawthorns and is another of Nature's provisions for maintaining balance. There are, of course, many other factors that tend to lessen the insect injury to the trees, such as the interrelations of the insects with their parasites and preyers, but so little is known about them that the writer makes no attempt to discuss them.

A host of bees, flies, and beetles visit the blossoms in quest of pollen and nectar. The winter buds in some species of hawthorn become coated with a sticky exudation, which attracts insects emerging in late winter, such as the stone flies and the chironomids. These transient members of the Crataegus fauna have been omitted from consideration in this paper. A list of insects that visit the blossoms is given by Knuth (1908).

In the preparation of the catalog of hawthorn insects it became noticeable that some of the species which have more than one host plant have chosen only closely related hosts, such as the apple, the pear, or the medlar, while many others have chosen their hosts from plants that grow in the same communities regardless of close botanical relationship. A study of these combinations of hosts and the habitats in which they grow has led the writer to believe that the hawthorns are members of at least five different plant communities, which may be described as follows:

1 Open woods. In woodlands where the growth habit of the taller trees permits sunlight to reach the ground so that an undergrowth may develop, such as that in a forest of oak, hickory, and elm, Crataegus is commonly found along with Corylus, Rhamnus, Carpinus, *Prunus spinosa*, and the like.

2 Deforested areas. Where a shrubby growth has sprung up after the destruction of a forest, numerous thorny forms such as Crataegus, Rubus, Berberis, and *Prunus spinosa* are frequently found.

3 Grazing lands. Hillsides or valleys where the soil is uncultivated and cattle are pastured are frequently dotted with Crataegus, Rosa, and crab apple, which because of their thorns can continue to thrive and outgrow the danger of being eaten by the cattle.

4 Stream banks. Just back of the willows and alders on moist alluvial soil beside streams, Crataegus grows to its greatest size and is associated with birch, willow, alder, and poplar.

5 Fence rows. Where shrubs are allowed to grow up along the fences, *Prunus virginiana*, Crataegus, wild plum, and wild cherry are frequently found closely associated.

In each of these five communities insects will be found which feed on the various plants of the community. For example, *Psylla mali* Schmid.

feeds on Crataegus, Malus, Sorbus, Quercus, Ulmus, and Corylus, which may all be found in the open-woods community, as may the host plants of the flat-headed apple-tree borer, *Chrysobothris femorata* Fabr. On the other hand, the leaf beetle, *Cryptocephalus bipunctatus* Linn., feeds near the streams on such plants as Salix, Betula, Crataegus, and Corylus, and *Agrilus vittaticollis* Rand. is found along the fence rows on Crataegus, *Prunus virginiana*, and Amelanchier. No very distinct lines can be drawn between the members of these communities, since many of the plants and insects belong to more than one community.

THE RELATION OF CRATAEGUS INSECTS TO APPLE, PEAR, AND QUINCE

A more complete knowledge of the insects that feed on Crataegus is of considerable importance as an aid in the control of insect pests of the cultivated commercial fruits. It has for many years, since the days of Walsh and Riley, been recognized by entomologists as the original native host plant of a number of important insect pests which now attack the apple, the pear, and the quince in the northeastern section of the United States. In all probability new pests must be expected to attack the cultivated fruits in the future as the population of the country increases since as a consequence less uncultivated land will remain where the insects may feed undisturbed on their natural hosts.

The main commercial fruits of the United States, such as the apple, the pear, the quince, and the cherry, are natives of the Old World and have been imported by man into America. With them were imported a number of foreign insects, such as the codling moth, the bud moth, and the sinuate pear borer, which continued to feed on them in this country. Many of the pests now destructive to these fruits, however, are native to North America and are not found in the Old World. Before the extensive planting of the imported fruits these insects must have fed on native plants. Among the most numerous of the native plants which are similar to the apple, the pear, and the quince are those of the genus Crataegus, and the members of this genus are widely distributed throughout many of our commercial fruit districts.

A young orchard which is set in the midst of hawthorns may be ruined in a few years by the insects that migrate to it from the surrounding trees. Well-established orchards may suffer from the attacks of new pests whenever there is a failure of the crop of wild haws or a clearing of the land occupied by hawthorns so that their natural guests must seek other hosts.

It is commonly known among entomologists that the apple maggot, *Rhagoletis pomonella*, was originally a hawthorn insect and that after the apple had been cultivated in North America for many years this insect selected the larger, juicier fruit of the apple for its home. It is still found in the haws but is now known as an apple pest.

The apple redbug, *Heterocordylus malinus*, is another hawthorn insect which has adopted the apple. It was formerly believed that the false apple redbug, *Lygidea mendax*, was also originally a hawthorn insect, but the observations of Cushman (1916), as well as those of the writer, indicate that *L. mendax* is a wild-crab insect and does not feed extensively on hawthorns.

The quince curculio, *Conotrachelus crataegi*, is a very common feeder in haws which has occasionally injured quinces seriously and has thus gained its common name. Likewise the lesser apple worm, *Laspeyresia prunivora*, has gained its common name because of occasional migrations from hawthorn to apple.

Baker (1915, 10) considers the woolly apple aphis, *Eriosoma lanigera*, to have been originally an elm-Crataegus feeder which has adopted the apple and traveled around the world with it. The woolly aphis is undoubtedly common on hawthorns.

Numerous other native American insects that feed on apple, pear, or quince are included in the catalog of hawthorn feeders beginning on page 1090.

The possibility that foreign hawthorn insects may be imported and become pests in North America should also be considered. When introduced into a new environment away from their natural checks, these may become more important here. Recent examples of this are three small moths imported from Europe—the apple and thorn leaf skeletonizer, *Simaethis pariana*; the hawthorn ermine moth, *Yponomeuta padellus*; and the lesser bud moth, *Recurvaria nanella*. These have attracted the attention of economic entomologists in North America as apple and cherry pests, while in Europe they feed commonly on hawthorns.

Since the catalog of hawthorn insects included in this memoir lists their food plants and the continents where each species occurs, further examples of foreign hawthorn insects that are now in North America may be found there.

BIOLOGICAL NOTES ON INSECTS FEEDING ON CRATAEGUS, AS OBSERVED BY THE WRITER FROM 1917 TO 1920[2]

ACARINA

Tetranychidae

telarius Linn., *Tetranychus* (Red spider)

The leaves of all species of Crataegus observed showed attack by *Tetranychus telarius*. The European hawthorns, however, seem to be more often severely injured by these mites than the native species. The

[2] The insects are grouped according to order and family, and arranged alphabetically by species within each family.

injury is severest in warm, dry periods. The leaves at first become grayish, due to the presence of a fine white web and the cast skins of the mites attached to them. Later they turn brown and their margins curl toward the surface on which the mites have fed. The adults hibernate among the fallen leaves and a few were found in bark crevices on the trunk in April. The tiny, round, white eggs are laid on the leaves. The mites breed continually on the leaves from June to October.

Eriophyidae

Eriophyes sp. No. 1 (Hawthorn serpentine gall of Jarvis)

The species of Eriophyes here described produces long, green or red serpentine galls confined to the space between two of the larger veins and extending from the midrib toward the margin of the leaf (fig. 102). The

FIG. 102.—LEAVES OF CRATAEGUS PUNCTATA SHOWING SERPENTINE GALLS PRODUCED BY ERIOPHYES SP. NO. 1

gall consists of a wavy projection on the upper side of the leaf and a wavy incision on the lower side. In cross section the leaf appears convoluted, with the galls projecting upward as loops or pockets in which the mites

live (fig. 103). The leaf does not become thickened in these galls. The galls become extremely abundant on some trees, so that almost every leaf is deformed. The mites seem to prefer the shady branches of trees, rather than those in bright sunlight. They become most abundant during August, when the galls are swarming with the microscopic white mites. The galls were found most abundantly on *Crataegus punctata*, but they were found also on *C. prunosa* and other native hawthorns.

FIG. 103 CROSS SECTION OF A CRATAEGUS LEAF, THROUGH THREE SERPENTINE GALLS

FIG. 104. HAWTHORN MARGINAL GALLS

Eriophyes sp. No. 2 (Hawthorn marginal gall)

Galls very similar to those of *Eriophyes goniothorax* Nal., which are found on hawthorns in Europe, are produced by *Eriophyes* sp. No. 2. The margin of the leaf is curled tightly downward for a distance of two centimeters or more (figs. 104 and 105), and the curled margin is paler green than the rest of the leaf. The mites live within the curl. This gall is not very common about Ithaca, but was found in a few cases on *Crataegus coccinea*.

Eriophyes sp. No. 3 (Thorn leaf pouch gall)

Many small, pale green pouches, standing on the upper side of the leaf and opening beneath the leaf by a small slit, are caused by microscopic white mites which live within the pouches. The galls vary in size and shape, but are generally about two millimeters high and are rounded on top (figs. 106 and 107). They may be found at any place on the leaf except on the larger veins. They are fairly common on *Crataegus punctata* but are not so abundant as the serpentine galls.

FIG. 105. CROSS SECTION THROUGH CURLED EDGE OF LEAF

FIG. 106. THORN LEAF POUCH GALLS

ORTHOPTERA

Acridiidae

atlanis Riley, *Melanoplus*
bivittatus Say, *M.*
femur-rubrum DeGeer, *M*

The common grasshoppers *Melanoplus atlanis*, *M. bivittatus*, and *M femur-rubrum* sometimes leave their herbaceous host plants to feed on the foliage of the lower branches of hawthorn trees. The older nymphs and adults have been observed feeding in August and September. They feed irregularly on the leaves, sometimes eating the entire leaf and sometimes eating only the apex or one side of it

HEMIPTERA

Miridae (Capsidae

communis Knight, *Lygus*

One adult of *Lygus communis* was taken on June 21 and four were taken on August 2, puncturing the leaves of *Crataegus punctata*.

dislocatus Say, *Horcias*

A few adults of *Horcias dislocatus* were found feeding on leaves of *Crataegus punctata* in June. They are black, rather stout, and 6 millimeters long

malinus Reuter, *Heterocordylus*
(Dark apple redbug)

Nymphs and adults of *Heterocordylus malinus* are very common on native hawthorns, where their red color and rapid running over the branches make them very conspicuous. The young nymphs begin to appear about April 15, when

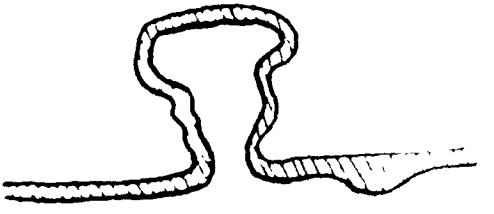


FIG. 107. CROSS SECTION THROUGH A THORN LEAF POUCH GALL

the blossom clusters have just begun to separate and before the blossoms show pink. They puncture the leaves and the tender twigs but do not cause any noticeable injury. After the fruit sets they feed on the fruit also and cause very slight dimples where they puncture it. They become adult in late May and early June, and begin ovipositing in the twigs about June 15. The egg is deposited in a small slit made with the beak at the base of a young twig. Adults were found on the trees until late July.

mendax Reuter, *Lygidea* (Bright apple redbug)

A few nymphs of *Lygidea mendax* were found feeding on the leaves and fruit of Crataegus in late April and in May. They are not so common as *Heterocordylus malinus*. In the warm laboratory the eggs hatched on March 27 on *Crataegus punctata* twigs, but no nymphs were found in the field until the blossoms were opening on April 25. Adults were found from June 2 to August 14. One adult in a breeding cage oviposited on June 19 in a twig of *Crataegus crus-galli*. She chose a year-old twig, drilled a hole through the bark at the base of the twig, and then, turning about, thrust an egg into the cavity.

ornatus VanD., *Orthotylus*

A few adults of *Orthotylus ornatus* were found feeding on the leaves of *Crataegus prunosa* in June. They are brownish, spotted, slender, and 5.5 millimeters long.

ostrya Knight, *Lygus*

A few adults of *Lygus ostrya* were taken puncturing the leaves of *Crataegus punctata* in late June. They are pale yellowish brown, and are otherwise similar in appearance to the tarnished plant bug.

pellucida Uhl., *Diaphnidia*

The pale green nymphs of *Diaphnidia pellucida* are rather numerous on the foliage of *Crataegus punctata* during late May and early June. They run rapidly over the branches when disturbed, and feed on the leaves and tender twigs. Adults appeared from June 10 to June 15 in rearing cages in the laboratory, and others were found in the field on June 18. They are delicate, slender, pale green, and about 4 millimeters long.

pratensis Linn., *Lygus*

Adults of *Lygus pratensis* which have lived through the winter are sometimes found puncturing the buds of Crataegus in April, as soon as the buds show green, and a few were found puncturing the young fruit in late May.

univittatus Knight, *Lygus*

Adults of *Lygus univittatus* are rather common during late May and June, puncturing the leaves and fruit of native hawthorns. They resemble *L. communis* very closely, but are generally paler.

Tingitidae

bellula Gibson, *Corythucha* (Plates LXXII and LXXIII)

Although the original description of *Corythucha bellula* was published but recently (Gibson, 1918), the species seems to be fairly common where its host plants occur, and it has probably been confused with *C. cydoniae* by earlier observers who must have seen it on the hawthorns. It has been found by Drake in Ohio and by Criddle in Manitoba.

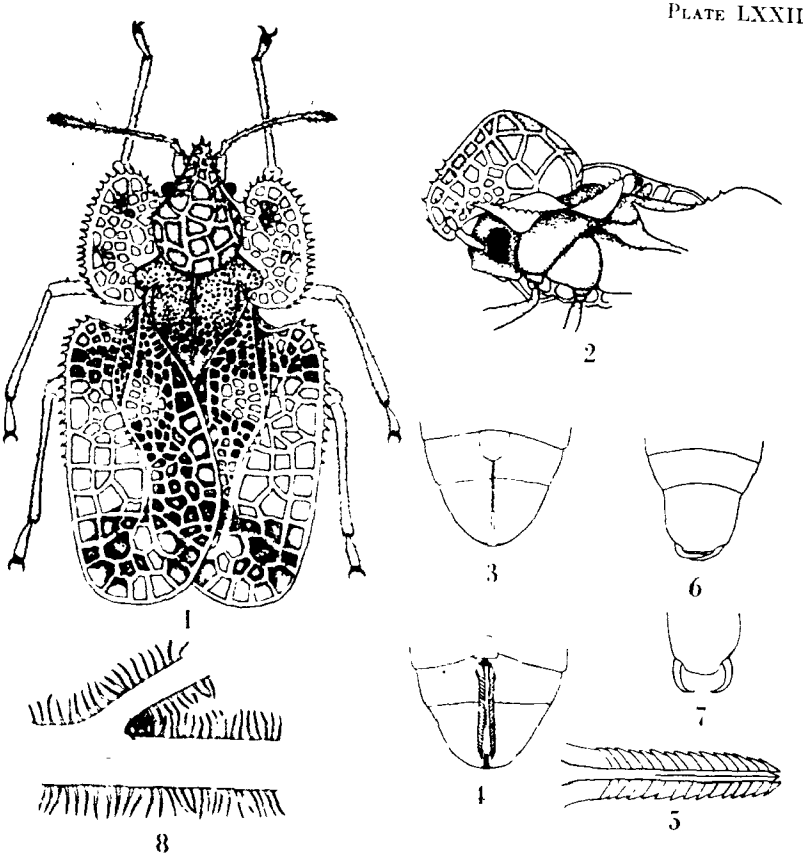
The host plants include those species of Crataegus that have hairy leaf veins, and also *Alnus incana* and *Ribes oxyacanthoides*. The writer has found the insect breeding in abundance on *Crataegus neoflavalis* and to some extent on *C. albicans* and *C. punctata*. The hawthorns with smooth leaves such as *C. prunosa*, *C. crus-galli*, and *C. oxyacantha*, even when their branches were intermingled with those of trees that were badly infested revealed no nymphs nor eggs.

In a large thicket of *C. neoflavalis* trees near the Cornell University campus, the leaves were so discolored by the end of July that they attracted attention several hundred yards away. By the middle of August the leaves were falling, and the branches were bare by September 1. No fruit matured on these trees. A few scattered trees of this species in other directions from the city were also badly infested. Individual trees of *C. albicans* and *C. punctata* showed an occasional branch badly infested and with leaves discolored. The injury is caused by the nymphs and the adults puncturing the under surface of the leaf and sucking the sap, producing at first a mottled effect due to the pale areas around the feeding punctures, while later the leaf turns brown and falls to the ground. Ornamental plantings of Crataegus in parks and gardens are rendered unsightly and weakened by this injury.

There are two generations annually at Ithaca. The first brood hatches in July from eggs laid in late May and in June, and the nymphs become mature in from twenty to twenty-five days. The second-brood eggs are laid in late July and in August, and the adults appear in late August and in September.

The adults of the second brood hibernate among the fallen leaves and in crevices of the bark. Many of them remain on the leaves on which they were feeding before the leaves fell. They appeared the last of May, and during early June were feeding on the new Crataegus leaves. As a rule only one pair of adults was found on a leaf, and they remained feeding and ovipositing on that same leaf for several days. After emergence from the nymphal skin in September, the adults of the second brood continue feeding on the leaves until they fall, in late September or in October.

The egg is subelliptical, with the basal end rounded and the apical end bent slightly to one side and capped with a rather broad cylindrical collar



CORYTHUCHA BELLUTA

1. Adult. 2. Lateral view of head and carina. 3. Tip of abdomen of female, with ovipositor at rest. 4. Same with ovipositor exserted; chitinized parts within body shown by dotted lines. 5. Ovipositor. 6. Tip of abdomen of male, with claspers at rest. 7. Same with claspers exserted. 8. Eggs in position among hairs in axil of leaf veins.

surmounted by a low cone with irregular ridges extending from base to apex. From the apex of this cone there arises in some cases a short, blunt prolongation, but often this is absent. The egg is without waxy covering over the chorion, which is smooth, unsculptured, and of a shining dark-brown color but somewhat lighter toward the base. The cap, or cone is often whitish. The egg, exclusive of the apical prolongation of the cap, is 0.52 millimeter long, and 0.21 millimeter broad at its greatest width.

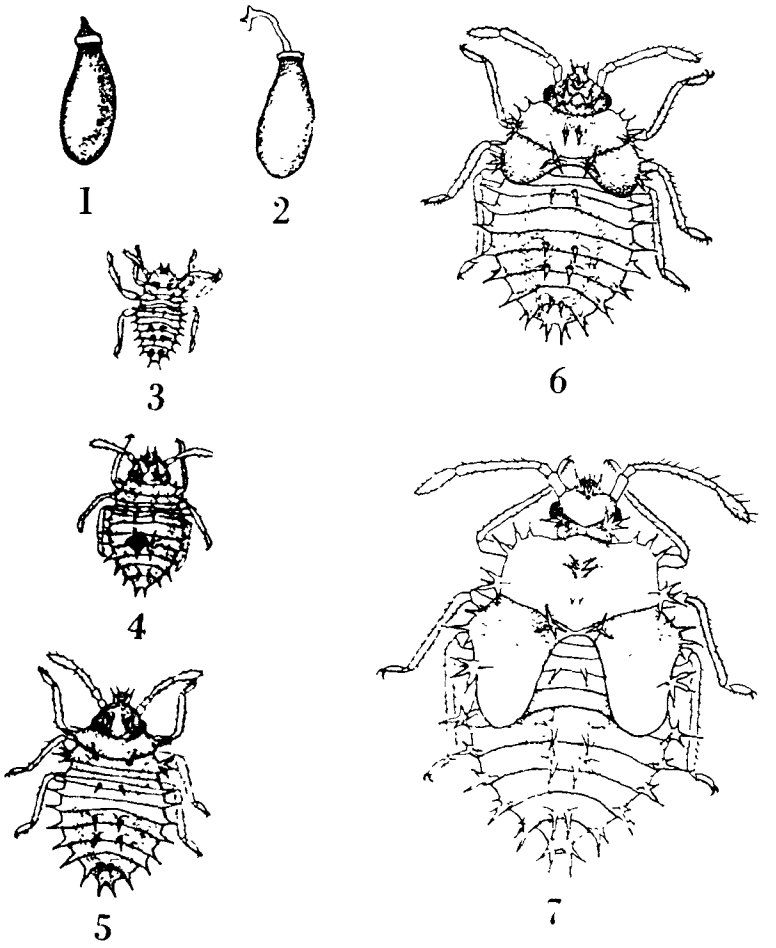
The eggs are laid on the under surface of the leaf, in the axils formed by the midrib and its lateral branches. Although the female has a well-developed, sawlike, four-valved ovipositor, the eggs are not inserted into the leaf tissue. They are placed among the hairs on the veins and are in some cases glued together with an adhesive material. They are generally laid in small groups, some groups containing as many as eighteen or twenty eggs; but occasionally they are laid singly. In counting the number of eggs on one hundred infested leaves the writer found an average of forty-nine eggs to a leaf. Occasionally a leaf had seventy-five or eighty eggs on it. The egg-laying period extends over several weeks, so that eggs, nymphs, and adults may be found at the same time in July and August.

Eggs laid on June 2 hatched on July 9 and 10, while the eggs of the second brood, laid on July 29 and 30, hatched on August 15 and 16. This indicates an incubation period of about thirty-seven days in the cooler temperature of June, and eighteen days in July and August when the average temperature was higher.

The conical egg cap is pushed up by the nymph as it begins to emerge from the egg still inclosed in the embryonic membranous sac. When about halfway out of the eggshell the nymph splits the membranous sac and slips it off over the head, leaving it with the egg cap on the outer end hanging out from the empty eggshell.

After emerging and drying, the nymphs begin to feed at once in colonies near the eggshells. They molt five times, feeding from three to six days between molts, the earlier stages requiring three or four days while the later ones require five or six days. In molting, the cuticula breaks along the median dorsal line from the front of the head to about the second abdominal segment. The insect on emerging is limp, and is almost colorless except for the eye facets which are bright red. The body color soon darkens and the eyes a few hours later become black. During the fifth stage the nymph wanders about more freely over the leaf and in some cases goes to adjoining leaves. Descriptions of the nymphal stages follow:

First stage.—Length 0.5 mm., greatest width 0.15 mm. General shape an elongate oval, somewhat broader cephalad than caudad and more elongate than in the later stages. Body first almost colorless but soon becoming dark brown. Beak 4-segmented and extending back to sixth abdominal segment. Antenna 3-segmented, the basal two segments subequal and shorter than the third segment, basal segment without spines or hairs, second segment with



YOUNG STAGES OF CORYTHUCHA BELLULA

1, Egg. 2, Egg after hatching. 3, First-stage nymph. 4, Second-stage nymph. 5, Third-stage nymph. 6, Fourth-stage nymph. 7, Fifth-stage nymph.

a few short hairs, third segment with numerous long spines and hairs, some with rounded tip and conical base, others with pointed tip. Head with five prominent dorsal tubercles, two slightly separated just above base of beak, each bearing a round-tipped spine; one tubercle back of these on median line bearing two spines, two tubercles near posterior margin, widely separated and each bearing two spines. Pro- and mesothorax having lateral tubercles with a spine on each, and mesothorax having a pair of dorsal tubercles with one spine on each. Metathorax and first abdominal segment without spines. Legs armed with short, pointed hairs and two bent, sharp, terminal claws. Nine abdominal segments visible above, each of these except the first bearing on each lateral margin a tubercle surmounted by a round-tipped spine, two dorsal tubercles on second, fifth, sixth, and eighth abdominal segments, these on second and eighth segments bearing one round-tipped spine each, and those on fifth and sixth segments bearing two spines each, tenth abdominal segment visible from a lateral or ventral view, this segment bearing no spines nor hairs, minute awl-shaped spinules over dorsal surface, especially on large tubercles of fifth and sixth abdominal segments and on thorax. (Plate LXXIII, 3)

Second stage. — Length 0.68 mm., greatest width 0.27 mm. Body broader in proportion to its length than in first stage, dark brown in color, with numerous minute spinules over dorsal surface, covering it much more completely than in first stage. Additional small spines on both dorsal and lateral tubercles, and the round-tipped spines present before having a slightly longer conical base in this stage. (Plate LXXIII, 4)

Third stage. — Length 0.82 mm., greatest width 0.44 mm. Antennæ with four segments. Round-tipped spines arising from a base longer than the spines, and a few additional small spines on tubercles. Pro- and mesothorax beginning to increase in prominence. (Plate LXXIII, 5)

Fourth stage. — Length 1.2 mm., greatest width 0.7 mm. Wing pads of mesothorax extending back over metathorax and first abdominal segment at sides. Prothorax more prominent than in earlier stages. Bases of round-tipped spines several times as long as the spines. A few new spines present on lateral margins of pro- and mesothorax and of abdomen. Color dark brown, except in an irregular band across abdomen just caudad of wing pads and on lateral thirds of prothorax, where it is yellowish. Minute spinules covering entire dorsum, light-colored on the yellowish parts and dark on the brown parts, these spinules present also on bases of round-tipped spines. (Plate LXXIII, 6)

Fifth stage. — Length 1.6 mm., greatest width 0.96 mm. Wing pads now extending back to fourth abdominal segment at sides, and prothorax still more prominent. A few more spines on tubercles, many of the sharp-pointed spines of the earlier stages now round-tipped, spines present in the earlier stages on lateral margins of segments covered by wing pads have disappeared. Yellowish parts of prothorax increased in size, and distal part of wing pads yellowish, giving the body the appearance of having two light bands across it. Entire dorsal surface covered with minute spinules as in earlier stages. (Plate LXXIII, 7)

In all stages of the nymphs the larger spines correspond exactly in position and shape with those so excellently described by Morrill (1905) for the oak lace bug, *Corythucha arcuata*. The only distinguishing characters between the nymphs of the two species which the writer has been able to observe are the size and the prevalence of minute awl-shaped spinules on the dorsal surface. Nymphs of *C. bellula* are smaller and possess more spinules, than those of *C. arcuata*. The larger spines of both species which are mounted on elongate bases seem to have an extensible sac on the tip which gives them a trumpet shape when it is drawn in and a round tip when it is extended.

The natural enemies of these spiny creatures seem to be few. Only the immature stages of several spiders were seen to prey upon them.

The webs of these spiders sometimes cover the infested leaves of a tree and entangle whole colonies of the lace bugs. The adults that survive the winter are comparatively few, so that the first brood of *C. bellula* does little injury.

Cicadellidae (Jassidae)

clitellarius Say, *Thamnotettix*

The adults of *Thamnotettix clitellarius* are of medium size, 5 millimeters long. They are yellow, with black wings which have a prominent yellow spot. A few specimens were found on June 11.

coccinea Först., *Graphocephala*

The adults of *Graphocephala coccinea* are 8 millimeters long, are slender, with a pointed head, and have the wings striped with alternate red and green. They are found on native hawthorns in July and August, but are not common.

curtisii Fb., *Euscelis*

The adults of *Euscelis curtisii* are small, 4 millimeters long, with many narrow yellow and black stripes. Specimens were found on June 23, but were not common.

fitchi VanD., *Idiocerus* (Black apple leaf hopper)

The adult of *Idiocerus fitchi* is 6 millimeters long, is brown or grayish with oblique white marks, and is found on native hawthorns in July and August. The black nymphs were reared on *Crataegus punctata* leaves from June 14 to July 2. The species winters in the egg stage.

lachrymalis Fb., *Idiocerus*

The adults of *Idiocerus lachrymalis* are 8 millimeters long, and are brownish or grayish mottled, with dark venation. They occur on native hawthorns in June and July. They are not common.

lineatus Linn., *Philaenus*

The adults of *Philaenus lineatus* are 6 millimeters long, brownish yellow, stout with a pointed head, and with a small black spot near the apex on the inner margin of the wing. They are found on native hawthorns from July 1 to July 15, but are not common.

mali LeB., *Empoasca* (Apple leaf hopper)

The adults of *Empoasca mali* are $3\frac{1}{2}$ millimeters long, slender, pale green. They are found rarely on Crataegus in late June.

obliqua Say, *Erythroneura*

The adults of *Erythroneura obliqua* are $2\frac{1}{2}$ millimeters long, with the wings striped red and white. They are very abundant on the leaves of native

hawthorns. They hibernate among the fallen leaves under the trees, and hundreds of them were present under *Crataegus punctata* trees in March, 1919. During warm days in winter they hop about over the leaves. Some individuals have pale pink stripes, and others reddish brown. Adults are found feeding on the trees in June and October.

pallidus Fb., *Idiocerus*

A single adult of *Idiocerus pallidus* was taken on June 23, on *Crataegus punctata*. It was 6 millimeters long, and was similar in size and shape to *I. fitchi* but was almost white.

provancheri VanD., *Idiocerus*

The adults of *Idiocerus provancheri* are 5½ millimeters long, and are brown or blackish with an elongate yellow spot on the base of the inner margin of the wing. They are common on the leaves of native hawthorns during June and July. Nymphs in the rearing cages hatched from eggs in *Crataegus punctata* twigs just as the buds were expanding in April. They became adult in three weeks.

querci Fitch, *Empoa*

The small, whitish leaf hoppers known as *Empoa querci* are very abundant on both native and imported hawthorns. The nymphs may be found on the under side of the leaves in late June and July, and again in September. The adults likewise occur on the under side of the foliage in June, August and late September or early October. They hibernate among the fallen leaves and become active on warm winter days. They are 3 millimeters long, and are pale yellowish white in color.

seminudus Say, *Eutettix*

The adults of *Eutettix seminudus* are 4½ millimeters long, rather stout, and white with a light brown band across the middle of the wings. They are rather common on *Crataegus punctata* and *C. tomentosa* foliage from mid-July to September.

suturalis Fb., *Idiocerus*

The adults of *Idiocerus suturalis* are 5½ millimeters long, and are pallid except for the black inner margin of the wings. They are found on native Crataegus in June and July, but are rare.

vanduzei Gill., *Euptery x*

The adults of *Euptery x vanduzei* are 2½ millimeters long, and are slender with a pointed head. The head, the thorax, and the apical part of the wings are brown, and the central part of the body and of the wings is greenish yellow. One nymph was taken on *Crataegus punctata* foliage and the adult emerged on August 15. The species is rarely found

vulgaris Fb., *Lamenia*

The adults of *Lamenia vulgaris* are 4 millimeters long, bluish gray, and rather stout. They are abundant on native hawthorns during the last half of June.

Membracidae

crataegi Fitch, *Glossonotus* (Hawthorn tree hopper)

The adults of *Glossonotus crataegi* are fairly common on the branches of native hawthorns during July and early August.

flavicephala Goding, *Ophiderma*

The adults of *Ophiderma flavicephala* are 8 millimeters long, are brown with a yellowish white stripe on each side and across the rear end of the prothorax, and are without a hump. They are rarely found on the branches of *Crataegus punctata* and *C. tomentosa* during June.

taurina Fitch, *Ceresa*

The adults of *Ceresa taurina* are 8 millimeters long, are pale green, and have the prothorax prolonged into a horn on each side of the head. They are found occasionally on the branches of *Crataegus punctata* and *C. neofluvialis* in late July and August. No nymphs were reared to the adult stage on Crataegus, but several nymphs answering the description of this species as given by Hodgkiss (1910) hatched on April 20 and lived through three instars on *Crataegus punctata* foliage.

Aphididae

corrugatans Sir., *Pemphigus* (Woolly thorn aphis)

A few colonies of the flocculent greenish aphids of the species *Pemphigus corrugatans* were found in early June on *Crataegus punctata*. They live on the under side of the leaves and curl the leaf margins downward.

crataegi Monell, *Macrosiphum*

The apterous females of *Macrosiphum crataegi* may be found from late May until October on the native hawthorns at Ithaca, and during July and August the species may become so abundant as to seriously injure the

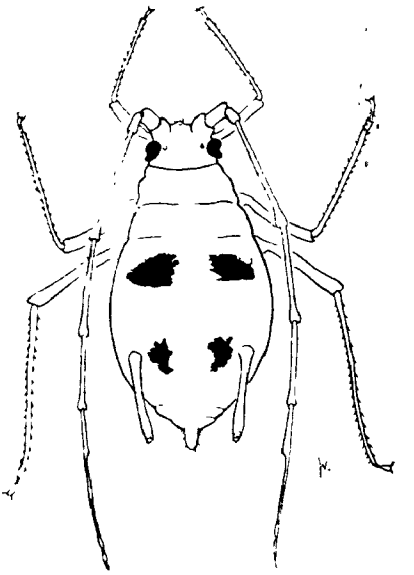


FIG. 108. MACROSIPHUM CRATAEGI

trees. During the summer of 1919 the writer saw a small *Crataegus pannosa* tree killed and a very large *C. punctata* tree almost entirely defoliated due to the sucking of sap by myriads of these aphids. They are rather large, yellowish green aphids, with long cornicles, and their most easily recognizable character is the presence of four dark green spots arranged in a rectangle on the dorsal side of the abdomen (fig. 108). The entire life history is passed on Crataegus trees. The black winter eggs are placed on the twigs and the smaller branches. They begin to hatch in May, after the leaves are well opened. The young aphids move to the lower surface of the leaves, and their feeding, as the colony increases, causes the leaves to curl downward.

In late June an alate brood appears and migrates to near-by branches or trees to start new colonies. It is after this brood appears that the species becomes so injurious.

crataegifoliae Fitch, *Aphis*

In early May, 1918, the *Crataegus coccinea* trees at Ithaca began to show the terminal rosettes of curled leaves caused by *Aphis crataegifoliae*. The rosettes turned red, and the aphids within them also were red. The infested branches remained deformed and somewhat stunted throughout the season, although the aphids departed from the trees about May 20 to seek leguminous hosts. No aphids of this species were observed the next year.

FIG. 109. ERIOSOMA LANIGERA ON HAWTHORN

lanigera Hausm., *Eriosoma* (Woolly aphis)

The woolly aphids first become noticeable in early June as small white spots on the tender twigs of Crataegus. In favorable season such as the summer of 1918 they become very conspicuous and cover entire branches by late summer. The writer has noted the roots of Crataegus infested.

pomi De Geer, *Aphis* (Green apple aphis)

During June and July the succulent sprouts of European and native hawthorns are badly infested by green apple aphids. Whenever the weather becomes unfavorable for their enemies they increase rapidly and infest entire trees or hedges, but fair weather checks them again.

prunifoliae Fitch, *Rhopalosiphum* (Apple bud aphis)

The dark green stem mothers of the species *Rhopalosiphum prunifoliae* begin to appear on the buds of native hawthorns as soon as the bud scales have separated enough to show the green leaves within. The colonies increase during April and early May, doing some damage to the young leaves and buds, but before June they migrate from the trees to grasses and are not often found on the trees between early June and late autumn. The winter eggs are laid on hawthorn twigs and buds.

Coccidae

corni Bouché, *Lecanium* (European fruit lecanium)

The species *Lecanium corni* is often very abundant on the lower side of branches of native hawthorns, and occasionally a branch is found to be almost entirely covered with these scales. Lower or inner branches that receive a scanty supply of light appear to be killed by them. The young, flat scales are sometimes very plentiful on the leaves in late summer.

furfura Fitch, *Chionaspis* (Scurfy scale)

The flat, whitish scale known as *Chionaspis furfura* is very common and noticeable on the bark of all Crataegus species which the writer has observed. The small, elongate, white, male scales are often very abundant on the leaves and bark of *Crataegus punctata*. The injury caused by these scales is not noticeable.

perniciosus Comst., *Aspidiotus* (San José scale)

Although the San José scale is fairly common on all species at Ithaca, it does not seem to increase rapidly enough to become injurious. It is more commonly found on the smooth bark of young trees than on old, rough-barked trees.

ulmi Linn., *Lepidosaphes* (Oyster-shell scale)

The oyster-shell scale is common on the bark of native and European hawthorns, and a few badly infested branches have been found. Generally, however, this species seems to be unimportant as a pest of Crataegus.

vitis Linn., *Pulvinaria* (Cottony scale)

The species *Pulvinaria vitis* is occasionally found on the twigs and branches of native hawthorns, but is not very abundant.

THYSANOPTERA

Thrypidae

tritici Fitch, *Euthrips*

Nymphs and adults of *Euthrips tritici* are very common in flowers and flower buds of native hawthorns in April and May. Many flower buds fail to open, and inside of them are found from one to a dozen or more of these thrips. They were exceedingly abundant in the Cornell University arboretum in 1918, and very few hawthorns there bore fruit that year.

COLEOPTERA

Elateridae

dubitans Lec., *Limonius*

The beetles of the species *Limonius dubitans* occasionally are found eating leaves of native hawthorns in late May and early June. On May 31, 1919, one of these click beetles was found on a *Crataegus punctata* leaf where it had been feeding, and was attacked by an adult pentatomid *Apateticus modestus* Dallas. The latter had its beak inserted into the beetle, which died while being carried to the laboratory.

pubescens Melsh., *Agriotes*

The beetles of *Agriotes pubescens* were eating the leaves of *Crataegus punctata* on May 23. The species is not common.

Melanotus sp.

The beetles of *Melanotus* sp. were eating the leaves of *Crataegus punctata* on June 6 and June 8. The species is not common.

Buprestidae

aeneus Melsh., *Brachys*

The beetles of *Brachys aeneus* were found feeding on *Crataegus punctata* leaves in warm sunlight from May 30 to June 20. There were commonly two or three to a leaf, feeding on the upper surface and cutting small holes through the leaf. As many as fifty of the beetles were found on one tree, while neighboring trees had none. They are from 4 to 5 millimeters long, and are brown and gold in color.

Scarabaeidae

elongata Fabr., *Dichelonycha*

The beetles of *Dichelonycha elongata* were found feeding on *Crataegus punctata* foliage, six being seen on one tree on May 31. A seventh beetle was killed by three adult pentatomids of the species *Apateticus* [illegible] which were feeding on its body.

testacea Kirby, *Dichelonycha*

The beetles of *Dichelonycha testacea* were found on *Crataegus tomentosa* foliage on May 29 and July 1. They cut irregular patches from the edge of the leaf. The species is not common.

Chrysomelidae

borealis Shev., *Diboliа*

The green flea beetles of the species *Diboliа borealis* are 2½ millimeters long. They feed on native hawthorn foliage in May, as soon as it is expanded. They hibernate beneath bark scales on the trunk and the branches, and when warmed in the hand in February they very soon become active.

carinata Germ., *Haltica*

The metallic violet or green flea beetles of the species *Haltica carinata* are 4 millimeters long. They feed on foliage of native hawthorns in June. They are not common.

cucumeris Harris, *Epitrix*

Tiny shining bluish beetles less than 2 millimeters long, of the species *Epitrix cucumeris*, were found feeding on *Crataegus punctata* foliage in June. The species is not common.

helxines Linn., *Crepidodera*

The shining greenish flea beetles of the species *Crepidodera helxines* are 3 millimeters long. They feed on the foliage of native hawthorns and are frequently so numerous as to cause considerable injury. They are found feeding in May, June, July, and August, but are most abundant in late May and in June. The beetles hibernate under bark scales on the trunk and the larger branches, where many of them die from the attack of a white fungous growth before spring.

marginalis Ill., *Systena*

Yellowish brown, slender flea beetles 4 millimeters long, of the species *Systena marginalis*, were found in August and early September eating holes in leaves of native hawthorns. The species is fairly common.

villosula Melsh., *Xanthonia*

The stout brownish or black beetles of the species *Xanthonia villosula* are 4 millimeters long. They were found feeding on the leaves of *Crataegus punctata* from late June to early August. Occasionally they are so abundant as to completely riddle the foliage of a tree with the holes they cut in feeding (Wellhouse, 1919). Feeding punctures are shown in figure 110, on the following page.

FIG. 110. FEEDING PUNCTURES OF XANTHONIA VILLOSULA IN LEAVES OF CRATAEGUS PUNCTATA

Curculionidae

crataegi Walsh, *Conotrachelus* (Quince curculio)

The square-shouldered brown beetles of *Conotrachelus crataegi* were found puncturing the fruit of Crataegus for feeding and oviposition in July and August, 1918, and in late May and June, 1919. The early months of 1919 were much warmer than those of 1918 at Ithaca, and this probably is the cause of the great variation in the time of their appearance. The larvae develop within the haws, feeding on the pulp surrounding the large, stony seeds. A larva commonly eats about one-half of the entire pulp of the fruit before emerging in the autumn, when it leaves the fruit by a large, round, exit hole. It then burrows down two or three inches in the soil and spends the winter as a larva curled in a smooth-walled earthen cell. In June, 1918, the writer found ninety-six larvae in the soil beneath one *Crataegus punctata* tree. Some of them pupated in June and others in July. They are very common on all the native hawthorns.

nebulosus Lec., *Anthonomus* (Hawthorn blossom weevil)

One of the most interesting and injurious of the insects found on the hawthorns is *Anthonomus nebulosus*, a member of a very destructive genus of blossom weevils. Its mode of life resembles in a general way that of the Mexican cotton boll weevil, *A. grandis*, and is almost identical with that of the European apple-blossom weevil, *A. pomorum* (Theobald, 1909, 104–110).

The original description of *A. nebulosus* is to be found in the Proceedings of the American Philosophical Society (Leconte, 1876), and a more complete description is given by Dietz (1891). In the present account it is

sufficient to say that *A. nebulosus* is a brown or grayish oval beetle, from 3.75 to 4.25 millimeters long, generally with a whitish, V-shaped mark on the fore part of the elytra, with a long, slender, curved beak, and the front femur having two teeth on its apical part, one large and the other small (Plate LXXIV, page 1070).

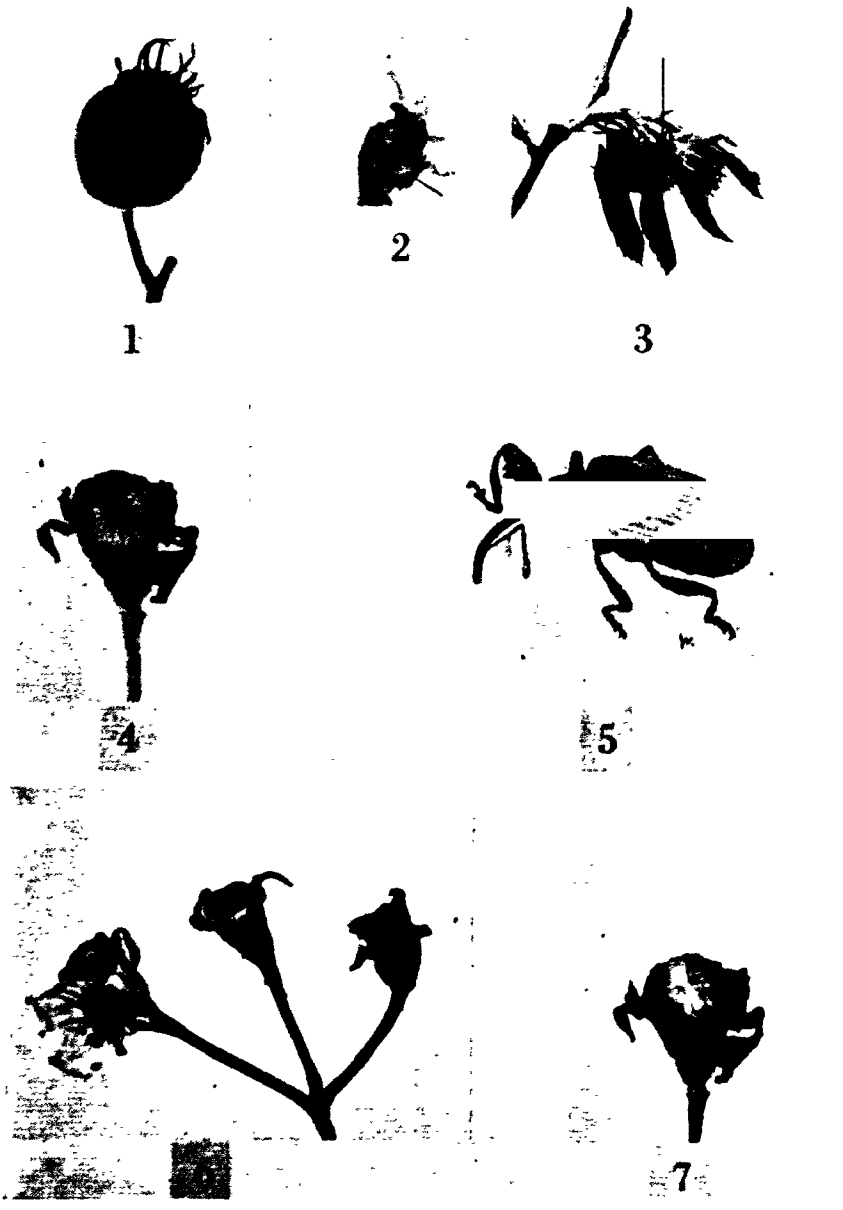
The species has been found in New York, New Jersey, Michigan, Indiana, Missouri, Arkansas, and Louisiana, and therefore it seems probable that it is present wherever its hosts are found east of the Rocky Mountains. Although Dietz considers this species to be more characteristic of the European fauna than of our own, no record can be found of its occurrence in Europe or elsewhere outside of this country.

Its hosts include a number of the larger-flowered species of hawthorns, such as *Crataegus punctata*, *C. brainerdi*, *C. pruinosa*, and *C. mollis*. The smaller-flowered species, such as *C. oxyacantha*, are not selected by the beetles for oviposition, probably because there is not space enough for the full development of the larva within the bud.

The injury caused by the hawthorn blossom weevil is most apparent while the trees are in full bloom. At that time the infested blossoms are brown and remain closed. On badly infested trees fully fifty per cent of the blossoms may be in this condition and the trees present a scorched appearance. As the young fruit begins to set, the infested blossoms commonly fall to the ground, but they may sometimes be seen on the trees even after the beetles have emerged in June.

The beetles come out of hibernation and appear on the branches of the hosts about mid-April, feeding ravenously on the buds, which are showing green. It is not uncommon to see a beetle with feet braced and beak inserted up to the eyes in a bud while it hurriedly eats the tender leaves within. As soon as all the food within reach of the entrance hole is eaten, the beetle seeks another bud on the twig and repeats the process. The puncture in the bud is round, is 0.3 millimeter in diameter, and turns dark as soon as the beak is withdrawn. The presence of the beetles may be detected by these dark round holes in the buds before the egg-laying period arrives. The beetles continue to feed on the buds during suitable weather until the clusters have separated enough for oviposition in the blossoms.

During cool weather the beetles remain inactive, generally in the axils of the twigs with their heads down. A few observations on the relation of temperature to their activities were made, and these indicate that the beetles remain inactive while the temperature is below 50° F. The optimum temperature is from 60° to 70°, and when it is raised to 78° the beetles rush about like mad, attempting to oviposit in every bud. Under most conditions they seem reluctant to fly, but when placed on distasteful food they fly away. They continue their activities on cloudy or rainy days and at night if the temperature is sufficiently high.



ANTHONOMUS NEBULOSUS

1. Feeding punctures of beetles in hawthorn fruit. 2. Egg in blossom bud. 3. Beetle ovipositing in blossom bud. 4. Flower with petals removed to show full grown larva in natural position. 5. Adult beetle. 6. Three flower buds containing larvae, and one open blossom. 7. Flower with petals removed to show pupa in its natural position.

The period between the opening of the blossom clusters and the opening of the blossoms themselves is the time of oviposition, and the length of this period probably influences the amount of injury to a considerable extent. If it is prolonged by cool, cloudy weather, then eggs may be placed in more of the blossoms before they open. In central New York the oviposition period is about May 15.

After selecting a suitable blossom bud, the female makes a hole in the side of the calyx with her beak. Then, turning around, she thrusts the egg into the hole with her ovipositor, and moves to another bud to repeat the process. A clear liquid fills the hole where the egg is thrust in, which soon hardens and seals the opening completely. The act of oviposition requires about ten minutes when the temperature is 68° or 70°, but it requires an hour at 54°.

The egg is pearly white, 0.6 millimeter long, 0.36 millimeter wide, elliptical, generally the same size at both ends but when tucked in tightly between the anthers it may be narrower at one end to conform to the space it fills. It is of almost the same size and color as the anthers and is difficult to distinguish from them. The corium is smooth, unsculptured, and delicate, drying and collapsing when exposed to the air for one hour.

After about a week the young, white, curved, legless larva is found within the bud. It feeds on the anthers, and, as it grows, consumes all the internal parts of the flower but leaves intact the wall of the receptacle and the closed petals which form the roof of its house. The petals become stiff as if they were starched, and do not shrink away as they turn brown. After feeding for a couple of weeks the larva is dirty white, is from 6 to 8 millimeters long, is still legless, has a small brown head, and lies in a curved position. At about this time it molts and changes to a white, free pupa 6 millimeters long, with a dark caudal spine, two dark prominent spines on the apex of the head, and several smaller spines farther back on the head. After pupating during a week or a little longer, the beetle makes a hole in the top or the side of its house with its beak, and emerges.

It begins to feed a few minutes after emergence, choosing for its food the first young thorn or fruit in its pathway as it wanders along the branch. The thorns of the current season's growth seem to be a very attractive food. A hole is drilled near the base of the thorn, and the beetle spends hours with its beak inserted in the hole completely up to its eyes, prying and straining to enlarge the cavity within the thorn. The round hole at the base of a thorn does not heal during the season's growth, and the presence of such holes will indicate at any time of the year the presence of the blossom weevils. The beetles attack the fruit also and make several round holes in a single fruit before seeking another. The holes become brown almost immediately. The writer has never found

the beetles eating leaves or tender twigs, but they sometimes feed on the succulent globular leaf galls of cecidomyiid larvae. They will puncture and feed on young apples in the cages when fresh haws are not to be had, but the writer has found none feeding on apples in the field.

After feeding for a week or ten days the beetles may be found in copulation on the branches, and a week or so later, as warm July weather comes, they disappear from the trees. Those kept in breeding cages remained hidden in fallen curled leaves and hollow twigs on the ground all summer and winter without feeding until the next spring. A search for their hiding places in the field revealed a score of the beetles inclosed in curled, dried leaves on the ground beneath their host trees.

The life cycle may be summarized as follows: The immature stages (egg, larva, and pupa) are completed within the closed blossom in from twenty-seven to thirty-five days, and the remainder of the year is passed in the adult stage. The adults feed on thorns and fruit for two or three weeks after emerging from the blossoms, and then remain quiescent among fallen leaves on the ground until the next spring, when they feed for about a month on the buds before ovipositing. Soon after oviposition the beetles die. In New York the eggs are laid about mid-May and the beetles emerge from the blossoms in June. W. D. Pierce, in a letter to the writer, says the beetles emerge in late March and early April in Louisiana. The time of their development in different latitudes is dependent on the opening of the hawthorn blossoms in these latitudes.

A number of natural enemies of the blossom weevil have been observed. Various birds, especially sparrows, pick open the brown blossoms to eat the larvae and the pupae. Pierce (1912, 77) found the weevils to be parasitized by *Catolaccus hunteri* and *Sigalphus* sp. The writer has bred another chalcid, *Habrocytus piercei* Cwfd., from the larva of the weevil, the adult parasites emerging on June 16 and 17.

quadrigibbus Say, *Tachypterus* (Apple curculio)

The four-humped brownish beetles of the species *Tachypterus quadrigibbus* were found occasionally feeding on the fruit of native hawthorns in June. Fruits of *Crataegus punctata* were put into rearing cages on June 25, and from these fruits five adults of this species emerged on July 15 and July 18.

LEPIDOPTERA

Papilionidae

turnus Linn., *Papilio* (Tiger swallowtail)

The green larvae of *Papilio turnus*, with their peculiar eye spots, were found feeding on the foliage of native hawthorns from June 20 to August 2. The species is not very common.

Saturniidae

io Fabr., *Automeris*

The eggs of *Automeris io* are not uncommon on the under side of hawthorn leaves in late June and in July. They are very characteristic and conspicuous. A cluster of eggs may consist of a dozen or more, each large and creamy white with a dark blue dot on the distal end. The larvae feed in colonies on the foliage during July, August, and September. They are at first dark, then green, and are always covered with a mass of dark, stinging spines.

Arctiidae

caryae Harris, *Halisidota* (Hickory tussock moth)

The black-and-white-tufted caterpillars of the species *Halisidota caryae* are fairly common on native hawthorns during August.

tessularis A. and S., *Halisidota*

The caterpillars of *Halisidota tessularis* are similar to those of *H. caryae* and are found occasionally on the foliage with them, but are not so common.

textor Harris, *Hyphantria* (Fall webworm)

A single colony of larvae of *Hyphantria textor* was feeding on *Crataegus pruinosa* on July 31, 1918. An egg cluster which was probably of this species hatched on June 19, and the young larvae fed on *C. punctata* leaves for a few days and then died.

Noctuidae

americana Harris, *Acronycta*

The larvae of *Acronycta americana* are green, with an abundant covering of yellowish white hairs and a few long pencils of black hairs. They were found feeding on the leaves of native hawthorns in late June and July. The species is not common.

dactylina Grote, *Acronycta*

The larvae of *Acronycta dactylina* are entirely covered with yellowish white hairs and have three long pencils of black hairs. They were feeding on the foliage of *Crataegus punctata* from August 15 to September. The species is not common.

lutecoma G. and R., *Acronycta*

The larvae of *Acronycta lutecoma* are black, with tufts of white hairs on segments 3 to 6 and tufts of black hairs on the other segments. They were found feeding on *Crataegus punctata* leaves from June 23 to July 22. The species is not common.

occidentalis G. and R., *Acronycta*

The larva of *Acronycta occidentalis* is hairy, with a dark head and dorsal stripes. The remainder of the body is at first whitish but in later stages is reddish. Larvae of this species were feeding on *Crataegus punctata* foliage from August 13 to September. The species is not common.

pyramidoides Guen., *Amphipyra*

The larva of *Amphipyra pyramidoides* is green, with a white dorsal and two yellow lateral stripes, and is found feeding on native hawthorn leaves in May. One larva constructed a silken cocoon among dead leaves on the ground on June 2 and the moth emerged on July 18. The species is not common.

radcliffei Harv., *Acronycta*

The larva of *Acronycta radcliffei* is greenish or black, has a dorsal line of green or brown with faint yellow and red lines, has a hump on segment 12, and is sparsely hairy. It feeds on the leaves of *Crataegus punctata* from June 29 to July 22. The species is not common.

superans Guen., *Acronycta*

The larva of *Acronycta superans* is green, with a black dorsal line widened into a spot on several abdominal segments and with the last segment angularly elevated. There are few hairs on the body. It was feeding on *Crataegus punctata* leaves from June 9 to July 1, and pupated in a silken cocoon among leaves and decayed wood on the ground. The moth emerged on July 23. Only one larva was found.

Notodontidae

concinna A. and S., *Schizura* (Red-humped apple caterpillar)

The brownish, red-humped larvae of *Schizura concinna* feed on leaves of native hawthorns during July, August, and early September. Occasionally they defoliate several branches of a tree, but they are not generally injurious as is *Datana ministra*. They seem to prefer apple to hawthorn. On July 27, 1918, a count was made of the infested trees in several thickets where seedling apples and hawthorns were growing together. Although the hawthorns were much more numerous than the apples, the latter had forty-six infested trees while the former had only three.

manteo Doub., *Heterocampa*

The larva of *Heterocampa manteo* is bright green marked with [illegible] was found feeding on the foliage of native hawthorns in late June July. The species is not very common. One larva taken from a *punctata* tree on August 15 continued to feed in the cage until Sep 2, when it wandered away to find a suitable place for spinning it

ministra Dru., *Datana* (Yellow-necked apple caterpillar)

One of the most destructive species to both native and European hawthorns during the past few years has been *Datana ministra*. Very few trees have escaped without at least one colony of these yellow-necked, black-bodied, gray-haired caterpillars feeding on a branch in July and August. Many trees have had an entire branch stripped bare of leaves, and occasionally a whole tree has been defoliated.

The light brown moths appeared and were found ovipositing during June and July. The clusters of white eggs, each cluster containing from 25 to 100, were deposited on the lower side of the leaves and were a common sight in July. The larvae of a colony begin to feed at the tip of a branch and migrate toward its base as they grow, leaving the bare branch behind them. As they become larger they scatter to adjacent branches and feed singly or by twos and threes. They become full-grown and enter the soil in September.

Several observations were made to determine whether the larvae prefer hawthorn to apple. When confined in cages they eat one as readily as the other. In the natural uncultivated areas where hawthorn, apple, and pear grow wild, however, it was noticed that the colonies of larvae were commoner on hawthorn than on the other trees. In one field containing 50 hawthorn, 39 apple, and 17 pear trees, 79 colonies of larvae were counted. Of these colonies 56 were on hawthorn, 15 on apple, and 8 on pear.

Lymantriidae

leucostigma A. and S., *Hemerocampa* (White-marked tussock caterpillar)

The larva of *Hemerocampa leucostigma*, with its bright red head, its red tubercles on segments 6 and 7 of the abdomen, its four white tussocks, and its three long, black pencils of hairs, is a common sight on both native and European hawthorns. It feeds on the foliage during June and July, and the hairy cocoons are common on the branches in winter.

Lasiocampidae

americana Harris, *Epicnaptera*

The large larva of *Epicnaptera americana* is gray with white spots and two red bands above, and orange with a row of lateral diamond-shaped black spots below. It feeds at night on *Crataegus punctata* foliage in July and August. The species is not common.

americana Fabr., *Malacosoma* (Apple tent caterpillar)

During the years 1917 to 1920, only the old egg masses of *Malacosoma americana* were found on the twigs of hawthorns about Ithaca. Only two colonies of larvae were seen on the favorite host, wild cherry, and only one colony on apple.

Geometridae

cognataria Guen., *Lycia*

The larva of *Lycia cognataria* is green and is 4½ centimeters long. It has two pairs of prolegs. On its head are blunt horns, and it bears a prominent red tubercle on the next to the last segment. It feeds on *Crataegus punctata* and *C. prunosa* foliage in July. It is not a common species.

magnarius Guen., *Ennomos*

A moth of *Ennomos magnarius* emerged from a brown silken cocoon on a twig of *Crataegus prunosa* on September 30. Eggs were found on a *C. punctata* twig on November 12. The brownish larvae, 5 centimeters long, were found occasionally in May and June.

pometaria Peck, *Alsophila* (Fall cankerworm)

The small greenish or brownish larvae of *Alsophila pometaria* are fairly common on native hawthorns in May.

subsignarius Hub., *Ennomos*

The white moths of *Ennomos subsignarius* emerged on July 6 and July 18 from pale yellowish pupae which were found tied with silk between the leaves of *Crataegus punctata*. A few of the brown and red larvae were found feeding on the foliage of native hawthorns in May.

tiliaria Harris, *Erranis* (Lime-tree spanworm)

The yellow-and-black-striped larvae of *Erranis tiliaria* are common on native hawthorn foliage in May and June.

titea Cram., *Phigalia*

Two larvae of *Phigalia titea* were found feeding on *Crataegus punctata* leaves on June 2 and June 5.

vernata Peck, *Paleacrita* (Spring cankerworm)

The larvae of *Paleacrita vernata* are common on foliage of native and European hawthorns in May and early June.

Sesiidae (Aegeriidae)

scitula Harris, *Sesia*

A single *Crataegus punctata* tree about eight years old and 5 inches high was killed by the larvae of *Sesia scitula*. The trunk was entirely girdled by four larvae which tunneled beneath the bark two inches above the soil. The sapwood was only slightly indented by their burrows and hardened. They pupated during June in silken cocoons covered with frass in the burrows, and the moths emerged from July 18 to July 21. In

ing, the moth pushes through one end of the cocoon, and then sheds the pupal skin while protruding about two-thirds of its length beyond the cocoon. The black, clear-winged moth has a broad and a narrow band of yellow across the abdomen.

Pyralidae

indigenella Zell., *Mincola* (Leaf crumpler)

The cornucopia-like winter cases of *Mincola indigenella*, a leaf crumpler, are easily seen on almost any hawthorn tree during the winter, attached firmly to the twigs and the branches and often with partly eaten leaves attached. The larvae carry the cases with them and feed on the leaves in April and May. They pupate within the same cases attached to twigs in June, and at Ithaca the moths emerge in late June.

Tortricidae

argyrospila Walk., *Archips* (Fruit-tree leaf roller)

The greenish larvae of *Archips argyrospila*, with their black heads and shields, are fairly abundant on the foliage of native hawthorns during May and are found occasionally in June. They tie together a cluster of leaves and feed on a leaf within the cluster. Moths emerged from the larval nests in late June and early July.

chionosema Zell., *Olethreutes*

The pale green larvae of *Olethreutes chionosema* fold the leaves of native hawthorns and feed on the upper surface of the leaves within the fold. Each larva folds a single leaf at a time. They are fairly common on the hawthorns and apple trees about Ithaca during May. The moths fly during June after pupating within the folded leaf. A few moths taken on August 14 and 15 seem to indicate a second brood. The moth (fig 111) is brownish, with a large white spot on the costal edge of the fore wing, and has a wing expanse of from 15 to 16 millimeters.

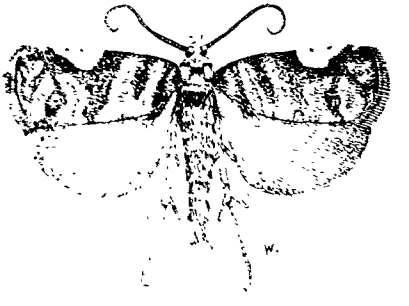


FIG. 111. OLETHREUTES CHIONOSEMA

nubeculana Clem., *Ancylis*

The greenish larvae of *Ancylis nubeculana* were found in late summer in rolled leaves of *Crataegus punctata*. They pupated in May and the moths emerged from June 8 to June 18. The species is not very common.

ocellana Fabr., *Tmetocera* (Bud moth)

The brownish larvae of *Tmetocera ocellana* are commonly found in the partly opened leaf buds in April and May, on both native and European hawthorns. The moths emerge from the larval nests in June and early July.

prunivora Walsh, *Laspeyresia* (Lesser apple worm)

The small white caterpillars of *Laspeyresia prunivora* are very common in the fruit of many native hawthorns in late summer. They eat most of the pulp from one side of the fruit, causing the skin to sink in there. The larvae of the second generation sometimes remain in the fruit all winter living within a mixture of silk and pellets of frass. Others spin silken hibernacula under the bark of the trunk very similar to those of the codling-moth larvae but smaller. They pupate within the hibernacula in the spring and the moths emerge in May and June. In the laboratory they emerged in March. Moths of the first generation were taken in the field from August 15 to August 30.

quadrifasciana Fern., *Eulia*

The yellowish larvae of *Eulia quadrifasciana* tie together with silk the leaves of terminal clusters on *Crataegus punctata* in May. They pupate within the larval nests and the moths emerge in early June. The moths yellow and orange, with darker oblique bands on the fore wings. The species is not very common.

rosaceana Harris *Cacoecia* (Oblique-banded leaf roller)

Clusters of leaves tied together by the larvae of *Cacoecia rosaceana* are fairly common on all native hawthorns in May and July. The green-striped larva, with its brown head and shield, is generally found on a single leaf under a slight web, feeding on one side of the leaf only. When full-grown the larva ties a cluster of leaves together to pupate within. Moths emerged from these nests from May 26 to June 30, and a second brood emerged from August 1 to August 15.

Yponomeutidae

areasella Clem., *Argyresthia*

The small, green, black-headed larva of *Argyresthia areasella* bores through a terminal leaf bud down into the twig and makes a hole in the side of the twig about ½ inch from the tip, through which the frass is cast out of the burrow. When disturbed the larva runs quickly out of the hole in the twig or the hole in the bud, to escape. Infested twigs wilt soon after the larva has left the burrow, and then become brown and dry, giving the tree a fire-blighted appearance (fig. 112). Larvae of this species were found in many native hawthorn twigs in May. They [illegible] the

twigs when full-grown, and spin a parchment-like white cocoon surrounded by an open layer of lacework attached to the surface of a leaf. The moths emerged from June 15 to June 30. A few moths taken in the field on August 16 seem to indicate a second brood. The moth is slender, and is white with oblique gold bands on the fore wings while the hind wings are dark gray. Its wing expanse is about 13 millimeters. It has a peculiar habit of standing on its head when at rest on the leaves or the bark.

FIG. 112. TERMINAL OF HAWTHORN TWIG DESTROYED BY LARVA OF ARGYRESTHIA OREASELLA

Elachistidae

fletcherella Fern., *Coleophora* (Cigar case-bearer)

The brown, cigar-shaped cases of the larvae of *Coleophora fletcherella* are common on all the hawthorns throughout the growing season. They have been specially abundant and injurious on trees and hedges of *Crataegus oxyacantha*, the European hawthorn, during the years 1918 and 1919. The moths emerged from the cases in late June and July.

malivorella Riley, *Coleophora* (Pistol case-bearer)

The curved cases of the larvae of *Coleophora malivorella* are fairly common on hawthorns but not so abundant as those of *C. fletcherella.*

splendoriferella Clem., *Coptodisca* (Resplendent shield-bearer)

The small, yellowish brown, winter shields of *Coptodisca splendoriferella* are rather commonly found attached to the bark and swinging in the wind on the branches of native hawthorns, and their blotch mines in the leaves are not uncommon.

Lyonetiidae

pomifoliella Clem., *Bucculatrix* (Ribbed-cocoon-maker of apple)

The elongate, white, ribbed cocoons of *Bucculatrix pomifoliella* are common on native hawthorns and are rather noticeable in winter, when the trees are leafless. The moths emerge in late May.

Cosmopterygidae

curvilinella Chamb., *Blastodacna* (Hawthorn fruit miner)

The larvae of *Blastodacna curvilinella* are very commonly found tunneling in the fruit of native hawthorns in late summer. They become full-grown in September and October, when they leave the fruit and burrow into the ends of dead twigs or other decaying wood to hibernate. The hibernation cavity is lined with silk, and in the early spring pupation takes place there. The moths emerge in May and June. They are gray, with two or three indistinct dusky longitudinal short streaks on the wings, and have a wing expanse of 1 centimeter.

The larva is from 9 to 10 millimeters long. In color it is yellowish white, with a brown head and thoracic legs, red spots near the spiracles, more or less blackish among the setae on the dorsum of each segment but especially noticeable on the prothorax and the anal segment, and many patches of black setae arranged as shown in figure 113. It feeds on the pulp of the fruit and leaves many brown pellets of excrement in the burrow behind it. Often one whole side of a fruit is mined out, leaving only the skin to cover it.

FIG. 113. LARVA OF BLASTODACNA CURVILINEELLA

The moths have been bred from larvae in *Crataegus prunosa*, *C. coccinioides*, and *C. macracantha*, and the larvae have been found in a number of other native hawthorns. The moth has been reported by Chambers from Kentucky (1872) and from Canada (1875), and therefore it probably occurs throughout the Eastern States.

A closely related European species, *B. hellerella* Dup., feeds in the fruit of hawthorns and also bores into young apple shoots (page 1116).

DIPTERA

Cecidomyiidae (Itonididae)

absobrina Felt, *Rhizomopa*

crataegifolia Felt, *Lestodiplosis* (Hawthorn fringed-cup gall)

Adults of both *Rhizomopa absobrina* and *Lestodiplosis crataegifolia* have been reared by Dr. Felt from larvae in the galls. The galls are green and cup-shaped, and are covered externally with round-tipped hairs. They are 4 or 5 millimeters in diameter and about the same in height (figs. 114 and 115). They occur on the larger veins and petioles of leaves and on the ends of young twigs of *Crataegus prunosa* and *C. macracantha*. Several galls are commonly found in a group on the same or adjoining leaves. Those on the leaves are on the upper side, but extend through the leaf to form a smooth, semi-globular swelling on the lower side.

FIG. 114. HAWTHORN FRINGED-CUP GALLS

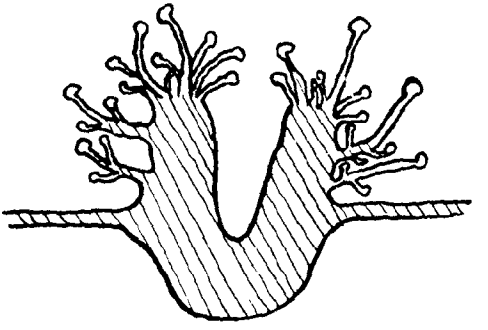


FIG. 115. CROSS SECTION THROUGH A HAWTHORN FRINGED-CUP GALL

White larvae, 3.5 millimeters long and with a distinct brown breast-bone, were found, one in each gall, in June.

FIG. 116.—THORN COCKSCOMB GALL

crataegifolia Felt, *Hormomyia* (Thorn cockscomb gall)

Green or red cockscomb-like galls (figs. 116 and 117) produced by *Hormomyia crataegifolia* are found on the upper or the lower side of leaves of *Crataegus punctata*, *C. macrosperma*, and *C. coccinea*. They are often in groups on a leaf or a cluster of leaves, and each gall includes a vein. The gall is from 8 to 12 millimeters long and 5 millimeters high and is open to the outside by a long, narrow slit on the opposite side of the leaf. These galls are found in August.

venae Felt, *Lobopteromyia* (Thorn vein gall)

Round or oval, thick-walled green galls (figs. 118 and 119) from 5 to 8 millimeters long, produced by *Lobopteromyia venae*, are found on either the upper or the lower surface of leaves of *Crataegus punctata*. The gall opens on the opposite side of the leaf by a narrow slit which extends the entire length of the gall in the direction of the vein. It always includes one of the larger veins. The galls are fairly abundant in June, when several may be found on one leaf and all the leaves in a cluster are deformed.

Cecidomyia sp. (a 1840 Felt) (Thorn spindle gall)

Red or green, elongate spindle-shaped galls (figs. 120 and 121) 2 millimeters wide and from 5 to 10 millimeters long, produced by *Cecidomyia* sp., are found on either side of the leaves of *Crataegus punctata*. The gall opens by

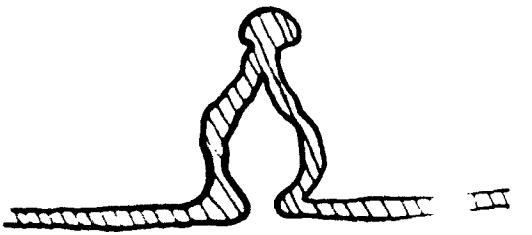


FIG. 117.—CROSS SECTION THROUGH A THORN-COMB GALL

FIG. 118. THORN VEIN GALLS

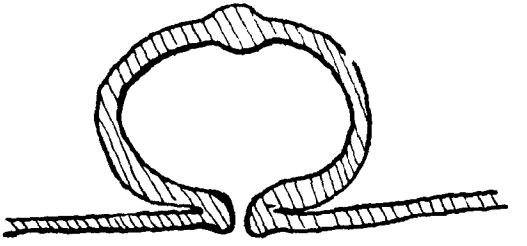


FIG. 119. CROSS SECTION THROUGH A THORN VEIN GALL

FIG. 120. THORN SPINDLE GALLS

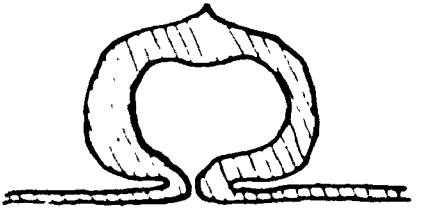


FIG. 121. CROSS SECTION THROUGH A THORN SPINDLE GALL

FIG. 122. PINEAPPLE GALLS

a long, narrow slit on the opposite side of the leaf. These galls occur very commonly in groups on the same leaf or on adjoining leaves. A single yellow larva, 1 millimeter long, and slender, is found in each gall in July or August.

Pineapple gall (maker unknown)

Red or green spiny galls, shaped and armored like a pineapple (figs 122, 123, and 124), 3 millimeters in diameter and 5 millimeters high, are found on the upper side of *Crataegus punctata* leaves in July and August. The pineapple gall is thick and is covered with fleshy spines at the base, but becomes slender, with long, slender spines, toward the apex, which is composed of two flat, leaflike, vertical plates. The gall opens between these two plates. Generally but one gall is found on a leaf and it is commonly on the midvein.

Trypetidae

pomonella Walsh, *Rhagoletis* (Apple maggot)

The maggots of *Rhagoletis pomonella* have been reared and flies obtained from the fruits of *Crataegus punctata*, *C. albicans*, *C. prunosa*, *C. brainerdi*, and *C. macrosperma*. The species probably lives also in the fruits of other large-fruited hawthorns. No larvae have been found in the small fruits of *C. neofluvialis* and *C. oxyacantha*, although these have been carefully watched. The maggots leave the fruit to enter the ground in autumn, and the flies emerge from the brown puparia in June and July.

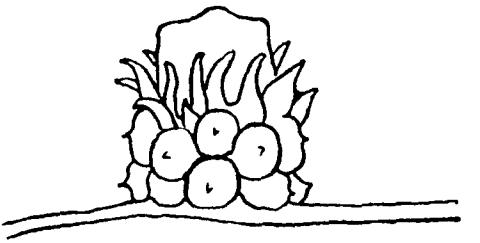


FIG. 123. SIDE VIEW OF PINEAPPLE GALL

All of the flies reared on hawthorns are equal in size to those reared on apple, not small like those reared on the blueberry. Counts were made of the infested and the uninfested fruits from a square yard beneath each of ten trees of the three species first mentioned in the preceding paragraph. The counts showed that from 20 to 25 per cent of the samples taken were infested by the maggots.

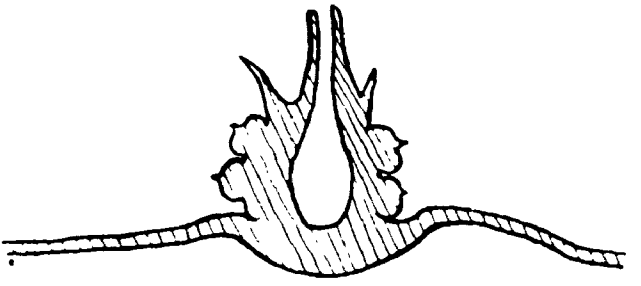


FIG. 124. CROSS SECTION THROUGH A PINEAPPLE GALL

HYMENOPTERA

Tenthredinidae

cerasi Linn., *Caliroa* (Pear and cherry slug)

The sluglike larvae of *Caliroa cerasi* were in a few localities so abundant that they defoliated a few native hawthorns and injured a number of others. In August, 1918, several trees on the Cornell University campus were completely defoliated, while neighboring trees were untouched by the larvae.

Sawfly No. 1

On June 23, 1918, a leaf of *Crataegus prunosa* was found with a row of fourteen eggs inserted in the margin. The eggs hatched on June 28 and a row of little green larvae, with large, black heads and many black dots scattered over the body, began to feed gregariously on the edge of the leaf. All of them died within a few days.

Sawfly No. 2

On May 24, 1918, several medium-sized sawfly larvae, bright green all over, were seen eating separately on the edges of *Crataegus* leaves.

Sawfly No. 3

Sawfly larvae, with red heads and yellow bodies marked with black lines and dots, were found feeding on the leaves of *Crataegus* in late August, 1918. They were feeding two or three together on and fifteen larvae were taken from one tree. When they became 2 centimeters long, on September 1 and 2, they spun brown cocoons on the ground among débris. A tree with ten larvae of the same

feeding on it was found on September 19, 1919, and these larvae spun cocoons on the ground on September 22 and 23.

Sawfly No. 4

A few larvae $2\frac{1}{2}$ centimeters long, with black heads and yellow bodies marked with black lines and dots, were found feeding on the foliage of *C. pruinosa* in July and August, 1918. They spun brown cocoons on top of the ground, in the cages.

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——— [*Blastodacna curvilinella*] *G. brevistatella*. N. sp. *In* Tineina from Canada. Canad. ent. 7: 210. 1875.

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GIBSON, EDMUND H. *Corythucha bellula* new species. *In* The genus Corythucha Stal. Amer. Ent. Soc. Trans. 44: 93–94. 1918.

HODGKISS, H. E. *Ceresa taurina* Fitch. *In* The apple and pear membracids. New York Geneva Agr. Exp. Sta. Tech. bul. 17: 100–105. 1910.

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Memoir 52, *Studies in Pollen, with Special Reference to Longevity*, the fourth preceding number in this series of publications, was mailed on March 9, 1922

CATALOG OF INSECTS INJURIOUS TO CRATAEGUS[1]

ACARINA

armatus Can., *Epetrimerus* — Fam. *Phyllocoptidae*
Host — *Crataegus oxyacantha.*
Injury — Forms galls on leaves
Distribution — Europe.
References — Houard, C. Les zoocecidies des plantes d'Europe, 1: 515. 1908
Theobald, F. V. Board Agr. London. Journ. 20: 106-116. 1913

calycobius Nal., *Eriophyes* — Fam. *Eriophyidae*
Host — *Crataegus oxyacantha.*
Injury — Deforms leaf buds and causes them to remain closed.
Distribution — Europe
Reference — Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911

crataegi Can., *Eriophyes* — Fam. *Eriophyidae*
Host — *Crataegus oxyacantha*
Injury — Forms galls on leaves, on both upper and lower surfaces. A single leaf may have a hundred galls on it
Distribution — Europe
Reference — Connold, E. T. British vegetable galls, p. 132. 1902

crataegi-vermiculus Walsh, *Eriophyes* — Fam. *Eriophyidae*
Hosts — *Crataegus tomentosa, C. coccinea*
Injury — Forms curled leaf galls on upper side of leaf
Distribution — North America
Reference — Walsh, B. D. Ent. Soc. Phila. Proc. 6: 227. 1866

gonathorax Nal., *Eriophyes* — Fam. *Eriophyidae*
Synonyms — *Eriocum oxyacanthae* Am., *Eriocum clandestinum* Grev.
Host — *Crataegus oxyacantha*
Injury — Forms galls on edges of lobes of leaf, causing them to curl downward and become thickened
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872
Connold, E. T. British vegetable galls, p. 138. 1902

pilosus Can., *Tetranychus* — Fam. *Tetranychidae*
Hosts — Crataegus, Malus, Pyrus, Prunus
Injury — Feeds on leaves, causing them to turn brownish.
Distribution — Europe, North America
Reference — Caesar, L. Can. ent. 47: 57. 1915

pyracanthae Link, *Eriophyes* — Fam. *Eriophyidae*
Hosts — *Crataegus punctata, C. pyracantha*
Injury — Makes galls on leaves. Galls almost flat, reddish, covered with [illegible] capitate hairs.
Distribution — North America
Reference — Chadwick, G. H. New York State Mus. Bul. 124: 131. 1908

pyri Pagst., *Eriophyes* (Pear leaf blister mite) — Fam. *Eriophyidae*
Hosts — Pyrus, Malus, Crataegus, Cydonia, Sorbus, Amelanchier.
Injury — Makes yellowish or reddish blisters on leaves.

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[1] The insects are grouped according to order, and arranged alphabetically by species with [illegible]

Distribution — Europe, North America, Australia
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 227. 1914.
Wilson, H. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2 123. 1915.

telarius Linn., *Tetranychus* (Red spider) Fam. *Tetranychidae*
(See page 1051.)

Eriophyes sp. (Hawthorn serpentine gall of Jarvis) Fam. *Eriophyidae*
Host — Crataegus.
Injury — Makes long, irregular, wavy galls on upper surface of leaves.
Distribution — North America.
Reference — Jarvis, T. D. Ent. Soc. Ont. Rept. 37 60. 1906.
(Figs. 102 and 103, pages 1052 and 1053.)

ORTHOPTERA

atlanis Riley, *Melanoplus* Fam. *Acrididae*
(See page 1054.)

bivittatus Say, *Melanoplus* Fam. *Acrididae*
(See page 1054.)

femur-rubrum De Geer, *Melanoplus* Fam. *Acrididae*
(See page 1054.)

niveus De Geer, *Oecanthus* (Snowy tree cricket) Fam. *Gryllidae*
Hosts — Malus, Rubus, Salix, Crataegus, Ulmus, Quercus, and other species.
Injury — Female slits bark to deposit eggs. Slits give entrance to cankers and cause scars on branches.
Distribution — North America, Cuba.
Reference — Parrott, P. J., and Fulton, B. B. New York (Geneva) Agr. Exp. Sta. Bul. 388. 1914.

ODONATA

viridis v. d. Lind., *Lestes* Fam. *Agrionidae*
Hosts — *Crataegus oxyacantha* and other species.
Injury — Oviposition punctures in twigs cause galls to form.
Distribution — Europe.
References — Pierre, P. F. M. Rev. sci. Bourbonnais 15 181. 1902.
Houard, C. Les zoocecidies des plantes d'Europe. 1 514. 1908.

HEMIPTERA

aceris Sign., *Phenacoccus* Fam. *Coccidae*
Hosts — *Crataegus oxyacantha* and many other woody plants.
Injury — Sucks sap from tender bark of young shoots and calloused wounds. Sometimes seriously injures grape.
Distribution — Europe.
References — Lindinger, L. Die Schildlause, p. 214. 1912.
Carpenter, G. H. Roy. Dublin Soc. Econ. proc. 2 142–160. 1914.

ambiguus Fall., *Psallus* Fam. *Miridae*
Hosts — Crataegus, Pyrus, Malus, Alnetis.
Distribution — Europe.
References — Reuter, O. M. Hemiptera gymnocerata Europae 1 105. 1878.
Leonardi, G. Gli insetti 4 98. 1901.

bakeri Cowen, *Aphis* (Clover aphid) Fam. *Aphididæ*
Hosts — Malus, Crataegus, clover.
Injury — Sucks juice from opening buds of fruit trees.
Distribution — North America.
References — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804: 15. 1917.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270: 19. 1918.

bellula Gibson, *Corythucha* Fam. *Tingitidæ*
Hosts — *Crataegus rectipratalis, C. punctata, C. albicans, Alnus incana, Ribes oxyacanthoides.*
Injury — Both young and adult bugs suck juice from leaves, causing them to turn brown and drop off.
Distribution — Northeastern United States, Canada.
References — Gibson, E. H. Amer. Ent. Soc. Trans. 44: 93. 1918.
Wellhouse, W. H. Journ. econ. ent. 12: 141. 1919.
Plates LXXII and LXXIII, pages 1057 and 1059.

betulae Bar., *Epidiaspis* (European pear scale) Fam. *Coccidæ*
Synonyms — *Epidiaspis lepeti* Signt., *E. pyricola* De Geer, *Diaspis pini* Colv.
Hosts — Pyrus, Malus, Prunus, Crataegus, and other species.
Injury — Very injurious to young twigs and branches of apple and pear in southern Europe, where the bark becomes incrusted.
Distribution — South and middle Europe, United States.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Essig, E. O. Injurious and beneficial insects of California, p. 172. 1915.

betuberculatum Targ., *Lecanium* Fam. *Coccidæ*
Hosts — *Crataegus oxyacantha*, Malus, Pyrus.
Injury — Sucks sap from bark, sometimes killing young trees.
Distribution — Europe, North America.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3: 695. 1913.
Dietz, H. F., and Morrison, H. Indiana State Ent. Ann. rept. 8: 251. 1916.

brevis Sand., *Aphis* (Long-beaked clover aphid) Fam. *Aphididæ*
Hosts — Crataegus, Cydonia, Pyrus, clovers, sweet pea.
Injury — Curls and turns purplish the terminal leaves of Crataegus shoots during late.
Distribution — United States.
Reference — Patch, E. M. Journ. agr. res. 3: 141. 1915.

brunneri Gibson, *Corythucha* Fam. *Tingitidæ*
Host — Crataegus.
Injury — Sucks juice from foliage.
Distribution — Southern United States.
Reference — Gibson, E. H. Amer. Ent. Soc. Trans. 44: 93. 1918.

bubalis Fabr., *Ceresa* (Buffalo tree hopper) Fam. *Membracidæ*
Hosts — Malus, Crataegus, and other species.
Injury — Adult makes incisions in branches for oviposition. Incisions do not heal and allow entrance of borers and fungi.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Hodgkiss, H. E. New York (Geneva) Agr. Exp. Sta. Tech. bul. 1: 10. 1910.

cistellarius Say, *Thamnotettix* Fam. *Cicadellidæ*
See page 1061

coccinea Forst., *Graphocephala* Fam. *Cicadellidae*
(See page 1061.)

communis Knight, *Lygus* Fam. *Miridae*
(See page 1054.)

corni Bouché, *Lecanium* (European fruit lecanium) . . . . . Fam. *Coccidae*
Hosts — Crataegus, Malus, Prunus, and other species.
Injury — May suck so much sap from branches as to kill them, but commoner injury is due to growth of sooty fungus over sticky secretion which the insects drop on foliage, fruit, and branches.
Distribution — Europe, North America.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3.695. 1913.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 261. 1914.

corrugatans Sir., *Pemphigus* (Woolly thorn aphis) . . . . . Fam. *Aphididae*
Hosts — Crataegus, Amelanchier, Pyrus, Cydonia.
Injury — Distorts leaves into a rolled curl.
Distribution — North America.
References — Patch, E. M. Maine Agr. Exp. Sta. Bul. 233. 1914.
Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804.19. 1917.

coryli Linn., *Lecanium* . . . . . Fam. *Coccidae*
Synonyms — *Eulecanium pyri* Schr., *Lecanium capreae* Linn.
Hosts — Malus, Crataegus, Pyrus, and other species
Injury — Sucks sap from bark, not commonly injurious.
Distribution — Europe, North America
References — Theobald, F. V. Insect pests of fruits, p. 175. 1909.
Lindinger, L. Die Schildlause, p. 216. 1912.

costalis Flor., *Psylla* . . Fam. *Psyllidae*
Hosts — Malus, Crataegus, Sorbus, Quercus.
Distribution — Europe.
References — Harrison, J. W. H. Naturalist (London), no. 707, p. 460. 1915.

crataegarium Walk., *Macrosiphum*. Fam. *Aphididae*
Host — *Crataegus oxyacantha*.
Distribution — England.
References — Walker, F. Ann. mag. nat. hist. 6.46. 1850.
Theobald, F. V. Journ. econ. biol. 8.142. 1913.

crataegi Kalt., *Aphis* Fam. *Aphididae*
Synonyms — *Aphis pyri* Boyer, A. *crataegi* Koch, A. *ranunculi* Kalt.
Hosts — *Crataegus oxyacantha*, *C. aestivalis*, Malus, Ranunculus.
Injury — Curls, discolors, and blisters leaves on terminal shoots.
Distribution — Europe.
References — Dobrovlianshy, V. V. Biology of aphids of tree and bush fruits (Kiev). 1913.
Van der Goot, P. Hollandischen Blattlause, p. 174. 1915.
Theobald, F. V. Entomologist 48.259. 1915.

crataegi Fitch, *Glossonotus* (Hawthorn tree hopper) . Fam. *Membracidae*
Hosts — Crataegus, Malus, Cydonia.
Distribution — North America.
References — Fitch, A. Third annual report on noxious insects of New York, p. 334. 1856.
Funkhouser, W. D. Cornell Univ. Agr. Exp. Sta. Memoir 11.248. 1917.

crataegi VanD., *Idiocerus* Fam. *Cicadellidæ*
Host — Crataegus.
Injury — Adults and young suck juice from foliage.
Distribution — North America.
Reference — Van Duzee, E. P. Can. ent. 22: 110. 1890.

crataegi Monell, *Macrosiphum* Fam. *Aphididæ*
Hosts — *Crataegus punctata*, *C. coccinea*, *C. oxyacantha*.
Injury — Sucks juice from lower side of leaves and from tender twigs. Leaves curl downward and in severe infestations trees may be defoliated.
Distribution — North America.
Reference — Patch, E. M. Maine Agr. Exp. Sta. Bul. 233: 255. 1914.
(Fig. 108, page 1063.)

crataegi Tullgr., *Prociphilus* Fam. *Aphididæ*
Hosts — *Crataegus oxyacantha*, Malus.
Injury — Curls and discolors leaves and sometimes injures blossoms.
Distribution — Europe.
Reference — Van der Goot, P. Hollandischen Blattläuse, p. 150. 1915.

crataegi Schr., *Psylla* Fam. *Psyllidæ*
Synonym — *Chermes quercus* Thoms.
Hosts — *Crataegus oxyacantha*, *Quercus* sp.
Injury — Causes small red blisters to form on upper side of leaves.
Distribution — Europe.
Reference — Aulmann, G. Psyllidarum catalogus, p. 13. 1913.

crataegi Dgl., *Typhlocyba* Fam. *Cicadellidæ*
Hosts — *Crataegus oxyacantha*, apple.
Injury — Nymphs and adults suck juice from foliage, but commonly they are not numerous enough to cause much injury.
Distribution — Europe.
References — Douglas, J. W. Ent. mo. mag. 12: 203. 1876.
Melichar, L. Cicadinen von Mittel-Europe, p. 348. 1896.

crataegiella Theobald, *Aphis* Fam. *Aphididæ*
Synonym — *Aphis crataegi* Buck.
Host — *Crataegus oxyacantha*.
Injury — Curls and discolors leaves of terminal shoots, which turn reddish brown.
Distribution — Europe.
References — Buckton, G. B. Monograph of British aphides, 2: 35. 1879.
Theobald, F. V. List of Aphididæ of Hastings District, p. 9. 1912.

crataegifolius Fitch, *Aphis* Fam. *Aphididæ*
Hosts — *Crataegus punctata*, *C. coccinea*, *C. oxyacantha*, *C. tomentosa*, Cydonia, Pyrus.
Injury — Curls and discolors leaves and young shoots, turning them purplish.
Distribution — North America.
Reference — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804: 18. 1917.

crataegus-coccinea Rafin., *Aphis* Fam. *Aphididæ*
Host — *Crataegus coccinea*.
Distribution — North America.
References — Rafinesque, C. S. Amer. mo. mag. and crit. rev. 3: 16. 1818.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270: 48. 1918.

curtum Fb., *Euscelis* Fam. *Cicadellidæ*
(See page 1161.)

cydoniae Fitch, *Corythucha*. . . Fam. *Tingitidae*
Synonyms — *Corythucha arcuata* Comst., *C. crataegi* O. & D.
Hosts — Crataegus, Cydonia.
Injury — Nymphs and adults suck juice from leaves, causing them to turn brown.
Distribution — North America.
References — Fitch, A. Country gent 17 25 1861.
Comstock, J. H. U. S. Ent. Rept. 1879 221. 1879.
Gibson, E. H. Amer. Ent. Soc. Trans. 44 87. 1918.

dearnessi King, *Phenacoccus*. . Fam. *Coccidae*
Synonym — *Phenacoccus bethelı* Ckll.
Hosts — Crataegus, Amelanchier
Distribution — Canada, United States.
Reference — Ferris, G. F. Contribution to knowledge of Coccidae of southwestern United States, p. 68. 1919.

dislocatus Say, *Horcias* Fam. *Miridae*
(See page 1054.)

dumetorum Schiff., *Physatocheila*. Fam. *Tingitidae*
Hosts — *Crataegus oxyacantha*, *Pyrus communis*, *Prunus padus*, *P. spinosa*.
Distribution — Europe, Egypt
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Saunders, E. Hemiptera of British Islands, p. 135. 1892.

edentula Buck., *Aphis* Fam. *Aphididae*
Host — *Crataegus oxyacantha*.
Distribution — Europe.
Reference — Buckton, G. B. Monograph of British aphides, 2 39. 1879.

fitchi VanD., *Idiocerus* (Black apple leaf hopper) Fam. *Cicadellidae*
Synonym — *Idiocerus maculipennis* Fitch.
Hosts — Crataegus, Malus, Pyrus
Injury — Adults and young suck juice from foliage. Not commonly injurious.
Distribution — North America.
References — Van Duzee, E. P. Catalog of Hemiptera, p. 580. 1916.
Brittain, W. H., and Saunders, L. G. Can ent. 49.149. 1917.

flavicephala Goding, *Ophiderma* Fam. *Membracidae*
(See page 1063.)

furfura Fitch, *Chionaspis* (Scurfy scale) . . . Fam. *Coccidae*
Hosts — About 25 tree species, including Crataegus, Malus, Pyrus, Cydonia, Sorbus.
Injury — Occasionally incrusts bark of trees and greatly weakens or kills them.
Distribution — North America.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 176. 1914.
Essig, E. O. Injurious and beneficial insects of California, p. 158. 1915.

hederae Vall., *Aspidiotus* . Fam. *Coccidae*
Synonym — *Aspidiotus nerii* Bouché.
Hosts — Many woody and herbaceous plants, including *Crataegus azarolus*.
Distribution — Europe, Asia, North Africa (on Crataegus in Algeria), North America.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:689. 1913.

lachrymalis Fb., *Idiocerus* . . . . . Fam. *Cicadellidae*
(See page 1061.)

lanigera Hausm., *Eriosoma* (Woolly aphis) . . . . . Fam. *Aphididae*
Synonyms — *Eriosoma crataegi* Oest., *Schizoneura americana* Riley.
Hosts — Crataegus, Malus, *Ulmus americana*.
Injury — Sucks sap from tender shoots, branches, and roots, often stunting growth
Distribution — North America, Europe, Africa, Australia, South America.
References — Theobald, F. V. Insect pests of fruits, p. 141. 1909.
Baker, A. C. U. S. Agr. Dept. Rept. 101. 1915.
Becker, G. G. Journ. econ. ent. 11: 245. 1918.
(Fig. 109, page 1064.)

lineatus Linn., *Phlaeus* . . . . . Fam. *Cicadellidae*
(See page 1061.

mali LeB., *Empoasca* (Apple leaf hopper . . . . . Fam. *Cicadellidae*
See page 1061

mali Schmid., *Psylla* . . . . . Fam. *Psyllidae*
Synonym — *Psylla crataegicola* Forst
Hosts — *Crataegus oxyacantha*, Malus, Pyrus, Sorbus, Quercus, Ulmus, Corylus
Injury — Nymphs suck juice from foliage and blossoms, and prevent setting of fruit
Distribution — Europe, Asia, Nova Scotia
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Theobald, F. V. Insect pests of fruits, p. 153. 1909.
Brittain, W. H. Journ. econ. ent. 15: 96. 1922.

malinus Reuter, *Heterocordylus* . . . . . Fam. *Miridae*
Dark apple redbug
Hosts — Crataegus, Malus
Injury — Nymphs and adults puncture leaves and fruit to suck juice. Cause dimples in fruit, which deform it
Distribution — Northeastern United States, Canada
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 28. 1914.
Cushman, R. A. Ent. Soc. Washington Proc. 18: 196. 1916.

maculata Oest., *Aphis* . . . . . Fam. *Aphididae*
Hosts — Crataegus, *Anthemis cotula*
Distribution — North America
References — Oestlund, O. W. Aphididae of Minnesota, p. 40. 1886.
Hunter, 1901, p. 101. (*Cited by* Patch, E. M. Maine Agr. Exp. Sta. Bul. 270: 49. 1918.

melanoneura Forst., *Psylla* . . . . . Fam. *Psyllidae*
Synonym — *Psylla crataegi* Forst
Hosts — *Crataegus oxyacantha*, Quercus, and other species.
Distribution — Europe, Asia
References — Aulmann, G. Psyllidarum catalogus, p. 20. 1913.
Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

mendax Reuter, *Lygidea* (Bright apple redbug . . . . . Fam. *Miridae*
Hosts — Malus, Crataegus
Injury — Nymphs and adults puncture leaves and fruit to suck juice, and cause dimples in fruit
Distribution — Northeastern United States, Canada
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 28. 1914.
Cushman, R. A. Ent. Soc. Washington Proc. 18: 196. 1916.

mespili v. d. G., *Ovatus* . . . . . Fam. [illegible]
Hosts — *Crataegus oxyacantha*, *Mespilus germanica*.

Injury — Sucks sap from tender shoots and leaves.
Distribution — Europe.
Reference — Van der Goot, P. Hollandischen Blattlause, p 136. 1915.

nigrofasciatum Perg., *Lecanium* (Terrapin scale) Fam. *Coccidae*
Hosts — Prunus, Acer, Malus, Crataegus, Tilia, Platanus, and other species.
Injury — Sucks sap from bark and secretes much sticky liquid, which covers surface of branches, foliage, and fruit and on which a sooty fungus grows, thus rendering fruit unsalable.
Distribution — North America.
References — Felt, E.P. New York State Mus. Memoir 8¹, 201. 1905.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 293. 1914.

obliqua Say, *Erythroneura* Fam. *Cicadellidae*
(See page 1061.)

olea Colvee, *Parlatoria* Fam. *Coccidae*
Hosts — Many woody plants, including *Crataegus germanica*.
Injury — May incrust the bark, and sometimes the leaves and the fruit, of trees of the genera Citrus, Pyrus, and Olea especially.
Distribution — Mediterranean region
References — Lindinger, L. Die Schildlause, p. 213. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3 694. 1913.

olivaceus Fabr., *Deraeocoris* Fam. *Miridae*
Synonym — *Capsus medius* Kirschb.
Hosts — Malus, Crataegus, Prunus, Corylus
Injury — Sucks juice from foliage
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Reuter, O. M. Hemiptera gymnocerata Europae 5:30. 1896.

ornatus VanD., *Orthotylus*. Fam. *Miridae*
(See page 1055.)

ostreiformis Curt., *Aspidiotus* (European fruit-tree scale) Fam. *Coccidae*
Synonym — *Aspidiotus oxyacanthae* Sign
Hosts — Malus, Prunus, Pyrus, Crataegus, and many other woody plants
Injury — May completely incrust the bark and kill the tree.
Distribution — Europe, Asia Minor, North America
References — Theobald, F. V. Insect pests of fruits, p. 386. 1909.
Lindinger, L. Die Schildlause, p. 213. 1912.

ostryae Knight, *Lygus* Fam. *Miridae*
(See page 1055.)

oxyacanthae Schr., *Myzus* Fam. *Aphididae*
Synonym — *Aphis oxyacanthae* Koch.
Hosts — *Crataegus oxyacantha*, Pyrus, Malus, Prunus
Injury — Sucks juice from leaves, causing yellow or red swellings on them and making them curl.
Distribution — Europe.
References — Koch, C. L. Pflanzenlause, p. 55. 1857.
Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911.

padi Linn., *Rhopalosiphum* Fam. *Aphididae*
Synonyms — *Aphis avenae* Fabr., *Aphis padi* Kalt.
Hosts — *Prunus padus*, Crataegus, Malus, Pyrus, grasses.

Injury — Sucks juice from opening buds of fruit trees in early spring.
Distribution — Europe, North America.
References — Leonardi, G. Gli insetti 4 228. 1901.
Baker, A. C. Journ. agr. res. 18 311. 1919.

pallidus Fb., *Idiocerus* . Fam. *Cicadellidae*
(See page 1062.)

pellucida Uhl, *Diaphnidia* . Fam. *Membracidae*
(See page 1055.)

peregrina Forst., *Psylla* Fam. *Psyllidae*
Synonym — *Psylla crataegicola* Flor.
Hosts — *Crataegus oxyacantha*, *Carpinus betulus*.
Injury — Sucks juice from young shoots and foliage.
Distribution — Europe, Asia.
Reference — Aulmann, G. Psyllidarum catalogus, p. 22. 1913.

perniciosus Comst., *Aspidiotus* San José scale. Fam. *Coccidae*
Hosts — Many woody plants, including Crataegus and other Malaceae.
Injury — May incrust bark and kill trees in favorable weather.
Distribution — Asia, North America, South America, Australia, Hawaii.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3 690. 1913.
Glenn, P. A. State Ent. Illinois Rept. 28 87. 1915.

piri Licht., *Aspidiotus* Fam. *Coccidae*
Hosts — Pyrus, Malus, Crataegus, Fraxinus, Prunus.
Injury — May incrust branches and thus weaken or kill them.
Distribution — Europe, Asia Minor.
References — Lindinger, L. Die Schildläuse, p. 214. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3 690. 1913.

pomi De Geer, *Aphis* Green apple aphis. Fam. *Aphididae*
Synonyms — *Aphis mali* Fabr., *A. oxyacanthae* Schr.
Hosts — Malus, Crataegus, grasses.
Injury — Sucks sap, causing leaves to curl, but no discoloration appears.
Distribution — Europe, North America.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 202. 1872.
Matheson, R. Cornell Univ. Agr. Exp. Sta. Memoir 24 686. 1919.

pratensis Linn., *Lygus* Fam. *Miridae*
(See page 1055.)

provancheri VanD., *Idiocerus* Fam. *Cicadellidae*
Hosts — Crataegus, Malus, Pyrus, Cydonia.
Injury — Nymphs and adults suck juice from foliage.
Distribution — North America.
References — Leonard, M. D. Journ. econ. ent. 8 415. 1915.
Van Duzee, E. P. Catalog of Hemiptera, p. 580. 1916.

prunicosum Coq., *Lecanium* (Frosted scale). Fam. *Coccidae*
Hosts — Many woody plants, including Crataegus.
Injury — Principal injury from smutty fungus growing on honeydew secreted by insects on fruit and foliage.
Distribution — North America.
References — Sanders, J. G. Journ. econ. ent. 2 442. 1909.
Essig, E. O. Injurious and beneficial insects of California, p. [illegible]. 1915.

prunifoliae Fitch, *Rhopalosiphum* Apple bud aphis. Fam. *Aphididae*
Synonyms — *Aphis avenae* (of American authors), *Aphis fitchii* Sand.

Hosts — Malus, Pyrus, Crataegus, Prunus, many grasses.
Injury — Sucks juice from opening buds of trees in spring.
Distribution — North America.
References — Quaintance, A. L. U. S. Ent. Bur. Circ. 81. 1907.
Baker, A. C. Journ. agr. res. 18 311. 1919.

pumilus Uhl., *Ceratocapsus* . . . Fam. *Miridae*
Synonym — *Melinna pumila* Uhl.
Hosts — Crataegus, Salix.
Injury — Adult sucks sap from foliage.
Distribution — Eastern United States
Reference — Uhler, P. R. Ent Amer 3 69. 1887.

pyri Fitch, *Prociphilus* (Pear root aphis) . . . . . .Fam. *Aphididae*
Hosts — Pyrus, Crataegus, Malus.
Injury — Sucks sap from roots.
Distribution — Eastern North America.
References — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804 19. 1917.
Wilson, H. F., and Vickery, R. A. Wisconsin Acad. Sci., Arts, and Letters. Trans. 19 149. 1918.

querci Fitch, *Empoa* . . . . . Fam. *Cicadellidae*
(See page 1052.)

rosae Linn., *Empoa* (Rose leaf hopper) . .Fam. *Cicadellidae*
Hosts — Rosa, Malus, Pyrus, Prunus, Crataegus, Cydonia, and other species.
Injury — Nymphs and adults suck juice from lower leaves of trees, causing yellowing of foliage and in some cases defoliation.
Distribution — Europe, North America.
Reference — Ackerman, A. J. U. S. Agr. Dept. Bul. 805. 20. 1919.

rumicis Linn., *Aphis* . . . Fam. *Aphididae*
Hosts — Many herbs and woody plants, including *Crataegus oxyacantha* and pear.
Injury — Sucks juice from foliage in spring and fall
Distribution — Europe, North America
References — Borner Nat. Ver. Bremen. Abhandl. 23 152. 1914.
Van der Goot, P. Hollandischer Blattlause, p. 220. 1915.

rusci Linn., *Ceroplastes* . Fam. *Coccidae*
Hosts — Many plants, including Crataegus
Injury — Sucks juice from bark, leaves, and fruit
Distribution — Mediterranean region
References — Lindinger, L. Die Schildlause, p. 214. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3. 695. 1913.

saliceti Först., *Psylla* . . . . . .Fam. *Psyllidae*
Hosts — Salix, *Crataegus oxyacantha*.
Injury — Sucks juice from foliage.
Distribution — Europe, Asia, Japan.
Reference — Aulmann, G. Psyllidarum catalogus, p. 23. 1913.

seminudus Say, *Eutettix* . . . .Fam. *Cicadellidae*
(See page 1062.)

sorbi Kalt., *Aphis* (Rosy apple aphis) . . . .Fam. *Aphididae*
Synonym — *Aphis malifoliae* Fitch.
Hosts — Malus, Pyrus, Crataegus, Sorbus, Plantago.
Injury — Curls leaves and deforms fruit.

Distribution — Europe, North America.
References — Van der Goot, P. Hollandischen Blattlause, p. 177. 1915
Matheson, R. Cornell Univ. Agr. Exp. Sta. Memoir 24: 718. 1919.

naturalis Fb., *Idiocerus* Fam. *Cicadellidæ*
(See page 1062.)

taurina Fitch, *Ceresa* Fam. *Membracidæ*
(See page 1063.)

ulmi Linn., *Lepidosaphes* (Oyster-shell scale) Fam. *Coccidæ*
Synonym — *Mytilaspis pomorum* Bouché
Hosts — Many woody plants, including Crataegus
Injury — Sucks juice from bark and foliage
Distribution — Europe, Asia, Africa, Australia, North America, South America, Hawaii
References — Theobald, F. V. Insect pests of fruits, p. 170. 1909.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3: 692. 1913.

ulmi Geof., *Tetraneura* Fam. *Aphididæ*
Hosts — Ulmus, *Crataegus oxyacantha*, many grasses
Injury — Sucks juice from leaves, causing galls to form on upper surface
Distribution — Europe
References — Van der Goot, P. Hollandischen Blattlause, p. 184. 1915.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270: 19. 1918.

unicolor Say, *Lygus* Fam. *Miridæ*
Host — Crataegus
Injury — Adults suck juice and puncture fruit and tender foliage
Distribution — Northeastern United States
Reference — Knight, H. H. Brooklyn Ent. Soc. Bul. 14: 21. 1919.

urticæ Linn., *Trioza* Fam. *Psyllidæ*
Hosts — Urtica, *Crataegus oxyacantha*
Injury — Sucks juice from foliage
Distribution — Europe, Asia
References — Ashmead, W. Psyllidarum Catalogus, p. 50. 1913.
Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

viridescens Gill., *Euphyllura* Fam. *Psyllidæ*
See page 1062.

vitis Linn., *Pulvinaria* (Cottony scale) Fam. *Coccidæ*
Synonyms — *Pulvinaria betulæ* Linn., *P. innumerabilis* Rath., *P. oxyacanthæ* Licht.
Hosts — Many woody plants, including Crataegus
Injury — Sucks sap from bark and tender shoots
Distribution — Europe, America, Africa, Asia Minor
Reference — Lindinger, L. Die Schildlause, p. 215. 1912.

vulgaris Fb., *Lamenia* Fam. *Cicadellidæ*
(See page 1063.)

THYSANOPTERA

tritici Fitch, *Euthrips* Fam. *Thripidæ*
See page 1066.)

COLEOPTERA

aeneovirens Marsh., *Rhynchites*, var. *punctatus* Oliv. Fam. *Curculionidæ*
Host — *Crataegus oxyacantha*
Distribution — Europe
Reference — Bargagli, P. Rincofori Europei, p. 181. 1883.

aenescens Lec., *Magdalis* (Bronze apple weevil) . .Fam. *Curculionidae*
Hosts — Malus, Crataegus, Prunus.
Injury — Larva tunnels under bark, sometimes killing tree. Adults feed on leaves.
Distribution — Northwestern United States, Canada
References — Chittenden, F. H. U. S. Ent. Bur. Bul. 22 37. 1900.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 199. 1914.

aequatus Linn., *Rhynchites* Fam. *Curculionidae*
Hosts — Crataegus, Malus, Prunus, Sorbus
Injury — Beetles puncture fruit buds and leaves in feeding.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 181. 1872.
Bargagli, P. Rincofori Europei, p. 181. 1883.

aerosus Melsh., *Brachys* . Fam. *Buprestidae*
(See page 1066.)

albida Lec., *Synuta* Fam. *Chrysomelidae*
Hosts — Malus, Pyrus, Cydonia, Crataegus, Prunus, Corylus, and other species.
Injury — Beetles feed on flowers and foliage, sometimes defoliating young trees.
Distribution — Western United States
References — Wilson, H. F., and Moznette, G. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2 96. 1915.

alpina Linn., *Rosalia* Fam. *Cerambycidae*
Hosts — *Crataegus oxyacantha*, *Fagus* sp.
Injury — Larva tunnels under bark, girdling branches, and then enters solid wood.
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Holeczek, A. Ent. Nachr. 13 308. 1887.

auratus Scop., *Rhynchites* Fam. *Curculionidae*
Synonym — *Rhynchites bacchus* Oliv.
Hosts — *Crataegus oxyacantha*, *Prunus spinosa*, Malus
Injury — Beetles cut off petioles of leaves, and larvae feed in fruit
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 153. 1872.
Bargagli, P. Rincofori Europei, p. 183. 1883.

bacchus Linn., *Rhynchites* (Purple apple weevil Fam. *Curculionidae*
Hosts — Malus, Crataegus
Injury — Larvae feed in fruit, much like codling moth.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Theobald, F. V. Insect pests of fruits, p. 121. 1909

barbicornis Lat., *Magdalis* (Apple stem piercer) Fam. *Curculionidae*
Hosts — Malus, Cydonia, Crataegus.
Injury — Larvae tunnel under bark, causing discolored, sunken areas.
Distribution — Europe, United States (New York and Massachusetts), imported recently.
References — Henschel, G. A. O. Die schadlichen forst- und obstbaum Insekten, p. 94. 1895.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 257. 1916.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

bipunctatus Linn., *Cryptocephalus* Fam. *Chrysomelidae*
Hosts — Crataegus, Corylus, Salix, Betula.

Injury — Beetles eat holes in foliage.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Kafer, p. 901. 1858.
Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.

borealis Shev., *Diboliu* . . . . Fam. *Chrysomelida*
(See page 1067.

calva Lec., *Limnobaris* Fam *Curculionidae*
Host — Crataegus.
Distribution — Eastern United States.
Reference — Hamilton, J. Amer. Ent. Soc. Trans. 22 377. 1895.

candida Fabr., *Saperda* Round-headed apple-tree borer Fam *Cerambycida*
Synonym — *Saperda bicallata* Say.
Hosts — Cydonia, Malus, Sorbus, Amelanchier, Pyrus, Crataegus.
Injury — Larvae tunnel under bark of trunk and into sapwood. Not commonly injurious to Crataegus.
Distribution — North America.
References — Glover, T. Manuscript notes from my journal, p. 87. 1877.
Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74 28. 1904.
Becker, G. G. Arkansas Agr. Exp. Sta. Bul. 146 5. 1918.

carinata Germ., *Haltica* Fam *Chrysomelida*
(See page 1067.

caudatus Rossi, *Otiorrhynchus* Fam *Curculionidae*
Host — *Crataegus oxyacantha*
Distribution — Europe.
References — Marseul, M. S. A. Monographie des Otiorhynchides, p. 127. 1872.
Bargagli, P. Rincofori Europei, p. 63. 1884.

cerasi Linn., *Magdalis* Fam *Curculionidae*
Hosts — *Prunus cerasus*, *P. spinosa*, *Crataegus oxyacantha*.
Injury — Larva burrows under bark.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Kafer, p. 758. 1858.
Bargagli, P. Rincofori Europei, p. 195. 1883.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

coeruleocephalus Schol., *Rhynchites* Fam *Curculionidae*
Hosts — *Crataegus oxyacantha*, Betula, Quercus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 589. 1872.
Bargagli, P. Rincofori Europei, p. 187. 1883.

colaspidoides Gyll., *Diphucephala* Fam *Scarabaeidae*
Hosts — Prunus, *Crataegus oxyacantha*.
Injury — Beetles appear in swarms, like locusts, and defoliate trees and shrubs.
Distribution — Australia.
References — Insect life 3 125. 1890.
French, C. Destructive insects of Victoria, 2 27. 1893.

convergens Lec., *Xylotrechus*. Fam *Cerambycida*
Host — *Crataegus* sp.
Injury — Larva, tunnels in branches.
Distribution — North America.
Reference — LeConte, J. L. Amer. Ent. Soc. Trans. 8 xxiv. 1880.

crataegi Walsh, *Conotrachelus* (Quince curculio) . . . . . Fam. *Curculionidae*
Hosts — *Crataegus* spp., Cydonia.
Injury — Larvae feed within fruit, partially destroying it.
Distribution — Eastern United States
References — Riley, C. V. Third Missouri rept., p. 35. 1871.
Slingerland, M. V. Cornell Univ. Agr. Exp. Sta. Bul. 148. 1898.

crataegi Germ., *Otiorrhynchus* . . . . . Fam. *Curculionidae*
Host — *Crataegus oxyacantha.*
Distribution — Europe.
References — Marseul, M. S. A. Monographie des Otiorhynchides, p. 287. 1872.
Bargagli, P. Rincofori Europei, p 63. 1883.

crataegi Walsh, *Pseudanthonomus* (Apple weevil) . . . Fam. *Curculionidae*
Hosts — Crataegus, Malus, *Kalmia latifolia.*
Injury — Larvae burrow in fruit, beetles puncture fruit and foliage.
Distribution — Eastern United States, Canada.
References — Brooks, F. E. West Virginia Agr Exp. Sta. Bul. 126. 1910.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 318. 1916.

cretata Newm., *Saperda* (Spotted apple-tree borer) . . Fam. *Cerambycidae*
Hosts — Malus, Crataegus, Amelanchier.
Injury — Larvae kill branches by girdling and tunneling in sapwood.
Distribution — Eastern North America.
References — Osborn, H. Iowa State Hort. Soc. Trans 15.11. 1880.
Hamilton, J. Amer. Ent Soc. Trans. 22 369. 1895.
Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74:50. 1904.

cucumeris Harris, *Epitrix* . . Fam. *Chrysomelidae*
(See page 1067.)

decipiens Lec., *Anthonomus* Fam. *Curculionidae*
Hosts — Crataegus, cotton (?), beetles in abundance beaten from *Crataegus* sp. by Dr. Hamilton.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 316. 1916.

dorsalis Thunb., *Chalepus* Fam. *Chrysomelidae*
Hosts — Robinia, Malus, Quercus, Crataegus, Rubus, and other species.
Injury — Beetles eat foliage.
Distribution — North America.
Reference — Houser, J. S. Ohio Agr. Exp. Sta. Bul. 332.231. 1918.

dubitans Lec., *Limonius* . . . . . Fam. *Elateridae*
(See page 1066.)

elongata Fabr., *Dichelonycha* . . . . . Fam. *Scarabaeidae*
(See page 1066.)

fayi Bland, *Saperda* (Thorn limb borer) . . . . . Fam. *Cerambycidae*
Hosts — *Crataegus crus-galli*, *C. tomentosa.*
Injury — Larvae burrow in smaller branches, killing them and producing gall-like swellings which weaken the branches so that they break in winds.
Distribution — Eastern North America.
Reference — Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74 62. 1904.

femorata Fabr., *Chrysobothris* (Flat-headed apple-tree borer) Fam. *Buprestidae*
Hosts — Many trees, including Crataegus, but especially Quercus, Malus, Prunus.

Injury — Larvae burrow in sapwood of weakened trees.
Distribution — North America.
Reference — Brooks, F. E. U. S. Agr. Dept. Farmers' bul. 1065: 5. 1919

flavicornis Boh. Schn., *Anthonomus* Fam. *Curculionidae*
Hosts — Crataegus, Solanum, dogwood, and other species.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of northeastern America p. 298. 1916.

flavicornis Clairv., *Ramphus* Fam. *Curculionidae*
Synonym — *Ramphus oxyacanthae* Marsh.
Hosts — Malus, *Crataegus oxyacantha*, Betula, Salix, Prunus, Populus.
Injury — Larvae mine in leaves.
Distribution — Europe.
References — Heyden, C. von. Berlin. ent. Zeit. 6: 63. 1862.
Bargagli, P. Rincofori Europei, p. 251. 1883.

foliacea Lec., *Haltica* = Apple flea beetle Fam. *Chrysomelidae*
Hosts — Malus, Crataegus.
Injury — Beetles and larvae eat many small holes in foliage.
Distribution — North America.
Reference — Murtfeldt, M. E. Insect life 1: 74. 1888.

gyarteus Krimek., *Rhynchites* Fam. *Curculionidae*
Host — *Crataegus oxyacantha*
Distribution — Europe, Asia.
References — Desbrochers, L. Monographie des Rhinomaceridae, p. 345. 1869.
Bargagli, P. Rincofori Europei, p. 180, 188. 1883.

helleri Lann., *Corythucha* Fam. *Tingitidae*
Hosts — Crataegus, Salix, Malus, Pyrus, Ulmus, Populus.
Injury — Beetles eat many small holes in leaves.
Distribution — Europe, North America.
References — Blatchley, W. S. Coleoptera of Indiana, p. 1214. 1910.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects p. 205. 1914.

coccinea Scop., *Rhynchites* Fam. *Curculionidae*
Synonym — *Rhynchites conicus* Ill.
Hosts — *Crataegus oxyacantha*, Malus, Pyrus, Prunus, Sorbus.
Injury — Beetles eat off tender twigs. Serious pest in nurseries.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 188. 1883.

impressifrons Gyll., *Polydrusus* Fam. *Curculionidae*
Hosts — Salix, Populus, Crataegus, Quercus, Malus, Pyrus, Corylus, and other species.
Injury — Beetles eat buds, leaves, and tender twigs in May and June.
Distribution — Europe, New York, imported about 1906.
References — Parrott, P. J., and Glasgow, H. New York (Geneva) Agr. Exp. Sta. Tech. bul. 50: 7. 1916.
Pierce, W. D. Journ. econ. ent. 9: 424. 1916.

mendicorvus Germ., *Phyllobius* Green leaf weevil Fam. *Curculionidae*
Hosts — Malus, Pyrus, Prunus, Quercus, Crataegus, Acer.
Injury — Beetle eats into opening buds, and later eats holes in leaves.
Distribution — Europe, Asia.
Reference — Theobald, F. V. Insect pests of fruits, p. 119. 1909.

marginalis Ill., *Systena*. Fam. *Chrysomelidae*
(See page 1067.)

metasternalis Cr., *Tymnes*. Fam. *Chrysomelidae*
Host — Crataegus.
Distribution — North America
Reference — Smith, J. B. Insects of New Jersey, p. 344. 1909.

mixtus Lec., *Anthonomopsis* Fam. *Curculionidae*
Hosts — Crataegus, Prunus
Distribution — North America
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 286. 1916.

multipunctata Say, *Calligrapha* Fam. *Chrysomelidae*
Host — Crataegus
Distribution — North America.
Reference — Blatchley, W. S. Coleoptera of Indiana, p. 1158. 1910.

naso Lec., *Conotrachelus* Fam. *Curculionidae*
Hosts — Crataegus, *Quercus virginiana*.
Injury — Larva feeds in fruit
Distribution — North America.
References — Hamilton, J. Can. ent. 21: 34. 1889.
Pierce, W. D. Nebraska State Bd. Agr. Ann. rept. 1906–07: 275. 1907.

nebulosus Lec., *Anthonomus* (Hawthorn blossom weevil) Fam. *Curculionidae*
(See page 1068.)

nenuphar Hbst., *Conotrachelus* (Plum curculio) Fam. *Curculionidae*
Hosts — Prunus, Pyrus, Malus, Cydonia, Crataegus.
Injury — Larvae feed in fruit, and beetles deform fruits by their feeding punctures.
Distribution — North America east of Rocky Mountains.
Reference — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 243. 1914.

nitidipennis Boh., *Magdalis*. Fam. *Curculionidae*
Hosts — Crataegus, Populus, Salix.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Kafer, p. 759. 1858.
Bargagli, P. Rincofori Europei, p. 196. 1883.

oblongus Linn., *Phyllobius* Fam. *Curculionidae*
Hosts — Malus, Crataegus, Populus, Corylus, and other species.
Injury — Beetles eat into opening buds, and later eat leaves.
Distribution — Europe, Asia.
Reference — Bargagli, P. Rincofori Europei, p. 79. 1883.
Theobald, F. V. Insect pests of fruits, p. 119. 1909.

olivaceus Gyll., *Rhynchites* Fam. *Curculionidae*
Synonym — *Rhynchites comatus* Dej.
Hosts — Crataegus, Corylus, Prunus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 190. 1883.

pauxillus Germ., *Rhynchites* Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Malus.
Injury — Beetles cut off twigs.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Theobald, F. V. Insect pests of fruits, p. 118. 1909.

politus Say, *Agrilus* Fam. *Buprestidae*
Hosts — Crataegus, Salix, Quercus, Corylus
Injury — Larva tunnels under bark, causing gall-like swellings on twigs of Crataegus and girdling twigs of oak with a spiral tunnel
Distribution — North America
References — Smith, J. B. Insects of New Jersey, p. 295. 1909.
Felt, E. P. New York State Mus. Bul. 200, 135. 1918.

pomonae Fabr., *Apion* Fam. *Curculionidae*
Hosts — Vicia, Crataegus
Distribution — Europe
References — Curtis, J. Farm insects, p. 187. 1860.
Bargagli, P. Rincofori Europei, p. 165. 1883.

pomorum Linn., *Anthonomus* Apple blossom weevil Fam. *Curculionidae*
Hosts — Malus, Pyrus, Crataegus
Injury — Larva feeds within closed fruit bud, destroying it. Often a very serious pest of apple in Europe. Whitehead records shaking 1530 adults from a single tree in two days.
Distribution — Europe, one specimen recorded from Ohio taken among [illegible]
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Dietz, Wm. G. Amer. Ent. Soc. Trans. 18: 204. 1891.
Whitehead, C. Report on injurious insects in Great Britain, p. 11. 1892.
Henschel, G. A. O. Die schadlichen forst- und obstbaum Insekten, p. 571. 1895.
Collinge, W. E. Manual of injurious insects, p. 97. 1912.

porcatus Boh. Schn., *Conotrachelus* Fam. *Curculionidae*
Hosts — Crataegus, Prunus, Carya
Injury — Larva feeds in fruit
Distribution — North America
References — Hamilton, J. Can. ent. 21: 34. 1889.
Blatchley, W. S., and Leng, C. W. Rhynchophora of northeastern America, p. 477. 1916.

profundus Lec., *Anthonomus* Fam. *Curculionidae*
Hosts — Crataegus, Quercus
Injury — Larva feeds in fruit
Distribution — North America
References — Blatchley, W. S., and Leng, C. W. Rhynchophora of northeastern America, p. 280. 1916.

prunt Ratz., *Ecoptogaster* Fam. *Ludiidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Ulmus
Injury — Larva girdles weakened trees by mining in cambium layer.
Distribution — Europe, Asia
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154. 1872.
Wahl, C. von. Borkenkafer an den Obstbaumen und ihre Bekampfung. Augustenberg Flugblatt, no. 3, p. 4. 1914.

prunt Linn., *Magdalis* Fam. *Curculionidae*
Hosts — Prunus, Crataegus, Rosa, and other species
Injury — Larva tunnels under bark of branches
Distribution — Europe, Asia

References — Bargagli, P. Rincofori Europei, p. 196. 1883.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

pterygomalis Boh., *Polydrusus*. Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Prunus, Salix, Betula, Corylus, Fagus.
Injury — Beetles feed on foliage.
Distribution — Europe, Asia.
Reference — Pierce, W. D. Journ. econ. ent. 9: 431. 1916.

pubescens Melsh., *Agriotes* Fam. *Elateridae*
(See page 1066.)

pubescens Fabr., *Rhynchites* Fam. *Curculionidae*
Synonym — *Rhynchites cyanicolor* Schr.
Hosts — Crataegus, Corylus, Alnus, Quercus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Bargagli, P. Rincofori Europei, p. 191. 1883.

quadrigibbus Say, *Tachypterus* (Apple curculio) Fam. *Curculionidae*
Hosts — Malus, Crataegus, Amelanchier, Pyrus.
Injury — Larva feeds in fruit, beetles puncture fruit and young twigs.
Distribution — Eastern North America.
References — Brooks, F. E. West Virginia Agr. Exp. Sta. Bul. 126. 1910.
Mitchell, J. B., and Pierce, W. D. Ent. Soc. Washington. Proc. 13: 53. 1911.

quercata Fabr., *Anthaxia* Fam. *Buprestidae*
Hosts — Crataegus, *Pinus strobus*, Cercis, and other species.
Injury — Larva bores in dead or dying branches.
Distribution — North America.
Reference — Knull, Josef N. Ent. news 31: 6. 1920.

rufus Ol., *Orchestes* Fam. *Curculionidae*
Hosts — Ulmus, Quercus, Salix, Crataegus, Prunus.
Distribution — Europe.
Reference — Bargagli, P. Rincofori Europei, p. 217. 1883.

rugulosus Ratz., *Eccoptogaster* (Fruit-tree bark beetle) Fam. *Ipidae*
Hosts — Prunus, Cydonia, Malus, Crataegus, Sorbus, Amelanchier.
Injury — Larva and adult mine in cambium layer of weak trees, frequently killing them.
Distribution — Europe, Asia, North America.
References — Gossard, H. A. Ohio Agr. Exp. Sta. Circ. 140. 1913.
Wahl, C. von. Borkenkafer an den Obstbaumen und ihre Bekamfung. Augustenberg Flugblatt, no. 3, p. 4. 1914.
Swaine, J. M. Can. Agr. Dept. Bul. 14: 52. 1918.

scheppardi Kirby, *Choragus* Fam. *Anthribidae*
Synonym — *Alticopus galeazii* Vill.
Host — *Crataegus oxyacantha*.
Injury — Larva burrows in dying twigs.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Kafer, p. 674. 1858.
Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.

sericeus Schal., *Polydrusus* Fam. *Curculionidae*
Hosts — Pyrus, Prunus, Crataegus, Malus, Fagus, Salix, Quercus, Alnus, and other species.
Injury — Beetles feed on buds and foliage.

Distribution — Europe, Asia, recently imported into United States (Indiana)
References — Kaltenbach, J. H. Pflanzenfeinde, p. 179. 1872.
Bargagli, P. Rincofori Europei, p. 59. 1883.
Pierce, W. D. Journ. econ. ent. 9: 428. 1916.

setiger Hbst., *Rhynchites* — Fam. *Curculionidae*
Synonym — *Rhynchites ophthalmicus* Steph.
Hosts — Crataegus, Corylus, Quercus, Betula
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 191. 1883.

sinuatus Oliv., *Agrilus* Sinuate pear borer — Fam. *Buprestidae*
Hosts — *Pyrus communis*, Crataegus, Sorbus
Injury — Larvæ tunnels in sapwood, making a zigzag mine
Distribution — Europe, North America
References — Smith, J. B. New Jersey Agr. Exp. Sta. Ann. rept. 15: 550. 1894.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3: 487. 1913.

subspinosus Fabr., *Macrodactylus* Rose chafer — Fam. *Scarabaeidae*
Hosts — Vitis, Malus, Pyrus, Rosa, Crataegus, and other species
Injury — Beetles feed on foliage, flowers, and fruit, and are sometimes very injurious
Distribution — North America
References — Hartzell, F. Z. New York, Geneva Agr. Exp. Sta. Bul. 331: 531. 1910.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 397. 1914.

testacea Kirby, *Lachnosterna* — Fam. *Scarabaeidae*
See page 1007

tomentosus Fabr., *Byturus* Raspberry beetle — Fam. *Lyctidae*
Hosts — Rubus, Crataegus, Malus, Pyrus
Injury — Beetles feed on flowers and foliage
Distribution — Europe
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3: 472. 1913.
Bot. journ., London 5: 73. 1917.

tubulatus Say, *Dinoderus* — Fam. *Ptinidae*
Hosts — Orchids, Crataegus
Distribution — North America
References — Pierce, W. D. Nebraska State Bd. Agr. Ann. rept. 1906-07: 281. 1907.
Blatchley, W. S., and Leng, C. W. Rhynchophora of northeastern America, p. 404. 1916.

villosula Melsh., *Xanthonia* — Fam. *Cerambycidae*
See page 1007

vittaticollis Rand., *Agrilus* — Fam. *Buprestidae*
Hosts — Crataegus, *Prunus virginiana*, Amelanchier
Injury — Beetles feed on foliage
Distribution — Eastern United States
Reference — Blanchard, F. Amer. ent. 3: 32. 1880.

Melanotus sp. — Fam. *Elateridae*
See page 1006

LEPIDOPTERA

abbotii Swains., *Sphecodina* — Fam. *Sphingidae*
Hosts — Vitis, Ampelopsis, *Crataegus tomentosa*
Injury — Larvæ feed on foliage

Distribution — Eastern North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Beutenmueller, William Hawk moths of the vicinity of New York City, p 12. 1903.

achatana Fabr., *Olethreutes* Fam. *Tortricidae*
Hosts — Crataegus, Malus.
Injury — Larvae roll leaves and eat them.
Distribution — Europe, Asia Minor
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Theobald, F. V Insect pests of fruits, p 81. 1909.

advenella Zk., *Rhodophaea* Fam. *Pyralidae*
Hosts — Crataegus, Pyrus
Injury — Larvae tie leaves and eat them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209 1872
Spuler, A Schmetterlinge Europas, 2 216. 1910.

aescularia Schiff., *Anisopteryx* (March moth) Fam. *Geometridae*
Hosts — Crataegus, Malus, Prunus, Pyrus, Quercus, Tilia, Ulmus, Acer, and other species.
Injury — Larvae feed on foliage, sometimes defoliating trees.
Distribution — Europe.
Reference — Theobald, F. V Insect pests of fruits, p. 61 1909.

americana Harris, *Acronycta* Fam. *Noctuidae*
(See page 1073.)

americana Harris, *Epicnaptera* Fam. *Lasiocampidae*
(See page 1075.)

americana Fabr., *Malacosoma* (Apple tent caterpillar Fam. *Lasiocampidae*
Hosts — Prunus, Malus, Crataegus, Sorbus, Rosa, Amelanchier, Quercus, Salix, and other species.
Injury — Larvae defoliate branches, living within a silken tent.
Distribution — North America.
References — Felt, E. P. New York State Mus. Memoir 8: 550. 1906.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 112 1914

anatipennella Hub., *Coleophora* Fam. *Elachistidae*
Synonym — *Coleophora tiliella* Zell.
Hosts — Crataegus, Quercus, Tilia, Corylus, *Prunus spinosa*
Injury — Larva eats patches of green tissue from leaf
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872
Spuler, A. Schmetterlinge Europas, 2 400. 1910.

anglicella Stt., *Ornix*. . Fam. *Gracilariidae*
Hosts — Crataegus, Fragaria.
Injury — Larva mines in leaf.
Distribution — Europe, Asia, one record in Massachusetts.
References — Stainton, H. T Natural history of the Tineina, 8 292. 1864.
Kaltenbach, J. H. Pflanzenfeinde, p. 171. 1872
Dietz, W. G. Amer. Ent Soc. Trans. 33 294. 1907.
Spuler, A. Schmetterlinge Europas, 2 410. 1910.

angustiorana Haw., *Capua* Fam. *Tortricidae*
Hosts — Crataegus, Laurus, Smilax, Pyrus, and other species

Injury — Larva ties leaves together and feeds on them.
Distribution — Southern Europe, northern Africa, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2: 246. 1910

antiqua Linn., *Notolophus* (Vaporer moth) Fam. *Lymantriidæ*
Hosts — Malus, Prunus, Rosa, Crataegus, Ulmus, Tilia, and other species.
Injury — Larvae defoliate branches.
Distribution — Europe, Asia, North America
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Theobald, F. V. Insect pests of fruits, p. 38. 1909.

argyrospila Walk., *Archips* (Fruit-tree leaf roller) Fam. *Tortricidæ*
(See page 1077

arthemis Dru., *Basilarchia* Fam. *Nymphalidæ*
Hosts — Crataegus, Salix, Tilia, Populus
Injury — Larvae eat leaves, except midrib, beginning at apex
Distribution — Eastern United States
References — French, G. H. Butterflies of the eastern United States, p. 208. 1886.
Edwards, H. U. S. Nat. Mus. Bul. 35: 27. 1889.

astyanax Fabr., *Basilarchia* Fam. *Nymphalidæ*
Hosts — Salix, Prunus, Malus, Tilia, Crataegus, and other species
Injury — Larva eats leaf on both sides of midrib, beginning at apex.
Distribution — Eastern and southern United States
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Holland, W. J. Butterfly book, p. 184. 1898.

aterrima Wek., *Nepticula*. Fam. *Nepticulidæ*
Host — *Crataegus oxyacantha*
Injury — Larva mines in leaf
Distribution — Germany
Reference — Spuler, A. Schmetterlinge Europas, 2: 480. 1910.

atricollis Stt., *Nepticula* Fam. *Nepticulidæ*
Hosts — *Malus malus, Prunus spinosa, Crataegus oxyacantha*
Injury — Larva mines in leaf
Distribution — Europe
Reference — Spuler, A. Schmetterlinge Europas, 2: 479. 1910

aurantiaria Esp., *Hibernia* Fam. *Geometridæ*
Hosts — Betula, Populus, Rosa, Quercus, Crataegus, and other species
Injury — Larva eats leaves
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209, 218. 1872.
Spuler, A. Schmetterlinge Europas, 2: 98. 1910.

bajaria Schiff., *Hibernia* Fam. *Geometridæ*
Hosts — Prunus, Pyrus, Crataegus, Ligustrum, Syringa
Injury — Larva eats foliage
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 196. 1872.
Spuler, A. Schmetterlinge Europas, 2: 98. 1910.

betulae Zell., *Lithocolletis* Fam. *Gracilariidæ*
Hosts — Crataegus, Pyrus, Cydonia, Betula
Injury — Larva mines in upper side of leaf
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 198. 1872.
Spuler, A. Schmetterlinge Europas, 2: 419. 1910.

betularia Linn., *Amphidasis* (Pepper-and-salt moth) . . . . Fam. *Geometridae*
Hosts — Malus, Prunus, Crataegus, Quercus, Ulmus, Populus, Betula.
Injury — Larvae defoliate trees in late summer.
Distribution — Europe, Asia, Japan.
Reference — Theobald, F. V. Insect pests of fruits, p. 64. 1909.

bidentata Clerck, *Gonodontis* (Scalloped hazel moth) . . Fam. *Geometridae*
Hosts — Corylus, Betula, Prunus, Crataegus, Pyrus, Quercus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia, Japan.
Reference — Collinge, W. E. Manual of injurious insects, p. 138. 1912.

biscutana Wck., *Epiblema* . Fam. *Tortricidae*
Hosts — Betula, *Crataegus oxyacantha*.
Injury — Larva ties together terminal clusters of leaves and feeds within.
Distribution — Norway, Finland.
Reference — Spuler, A. Schmetterlinge Europas, 2 283. 1910.

blandula Hulst, *Catocala* Fam. *Noctuidae*
Host — Crataegus.
Injury — Larvae feed on foliage.
Distribution — Eastern United States, Canada.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 533. 1890.
Smith, J. B. Insects of New Jersey, p. 476. 1909.

brumata Linn., *Cheimatobia* (Winter moth) Fam. *Geometridae*
Hosts — Fruit and forest trees (except conifers) and shrubs.
Injury — Larvae defoliate trees and may attack flowers or fruit.
Distribution — Europe, Asia, Greenland.
References — Ormerod, E. A. Manual of injurious insects, p. 338, 360. 1890.
Theobald, F. V. Insect pests of fruits, p. 50. 1909.
Med. Phytopath. Dienst. Wageningen, no. 3. 1916.

calanus Hub., *Strymon* (Banded hair-streak) Fam. *Lycaenidae*
Synonym — *Thecla falacer* Godart.
Hosts — Crataegus, Quercus, Hicoria.
Injury — Larva eats holes in leaves
Distribution — United States and Canada.
References — Scudder, S. Butterflies of New England, 2. 885. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

caryae Harris, *Halisidota* (Hickory tussock moth) . . . Fam. *Arctiidae*
Hosts — Hicoria, Juglans, Malus, Cydonia, Crataegus and other species.
Injury — Larvae eat foliage.
Distribution — United States east of Rocky Mountains.
Reference — Soule, Caroline G. Psyche 6. 158. 1891.

catax Linn., *Eriogaster*. . . . Fam. *Lasiocampidae*
Hosts — Crataegus, Quercus, Populus, Betula.
Injury — Larvae defoliate branches, which they cover with silken tents.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 1. 117. 1908.

cecropia Linn., *Platysamia* . Fam. *Saturniidae*
Hosts — Crataegus, Malus, Pyrus, Prunus, Salix, Acer, Syringa, and other species.
Injury — Larva eats leaves.
Distribution — North America east of Rocky Mountains.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Dickerson, Mary C. Moths and butterflies, p. 157. 1901.

cerisolella Pey., *Lithocolletis* — Fam. *Gracilariidae*
Hosts — Crataegus, *Sorbus torminalis*.
Injury — Larva mines in leaf on under side.
Distribution — Southern France.
Reference — Spuler, A. Schmetterlinge Europas, 2 415. 1910.

chionosema Zell., *Olethreutes* — Fam. *Tortricidae*
(See page 1077.)

chrysorrhea Linn., *Euproctis* (Brown-tail moth) — Fam. *Lymantriidae*
Hosts — Crataegus and most other deciduous trees.
Injury — Larvae defoliate trees.
Distribution — Europe, Asia Minor, New England States.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872
Spuler, A. Schmetterlinge Europas, 1 132. 1908.

clerkella Linn., *Lyonetia* — Fam. *Lyonetiidae*
Hosts — Pyrus, Prunus, Crataegus, Sorbus, Betula.
Injury — Larva makes serpentine mine in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2 422. 1910.

coerulocephala Linn., *Laloba* (Figure-8 moth) — Fam. *Noctuidae*
Hosts — Malus, Prunus, Crataegus, and other species.
Injury — Larva eats foliage, sometimes defoliating hawthorn hedges.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872
Theobald, F. V. Insect pests of fruits, p. 35. 1909

cognataria Guen., *Lycia* — Fam. *Geometridae*
(See page 1076.)

cognatellus Hub., *Yponomeuta* (Hedge ermine moth) — Fam. *Yponomeutidae*
Hosts — *Crataegus oxyacantha*, Euonymus.
Injury — Larva eats leaves, sometimes stripping hedges.
Distribution — Europe.
References — Spuler, A. Schmetterlinge Europas, 2 144. 1910.
Noel, P. Jardinage 4 363. 1914

concinna A. and S., *Schizura* (Red-humped apple caterpillar) — Fam. *Notodontidae*
Hosts — Malus, Crataegus, Prunus, Pyrus, and other species.
Injury — Larvae defoliate branches, feeding in a colony.
Distribution — North America.
References — Saunders, William. Can. ent. 13 139. 1881.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 125. 1914

concomitella Bnks., *Lithocolletis* — Fam. *Gracilariidae*
Synonym — *Lithocolletis pomifoliella* Zell.
Hosts — Malus, Crataegus.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 198. 1872.
Spuler, A. Schmetterlinge Europas, 2 415. 1910.

congelatella Clerck., *Exapate* — Fam. *Tortricidae*
Hosts — Crataegus, Sorbus, Prunus, Pyrus, Rubus, Berberis, Ligustrum, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2 254. 1910.

contaminana Hub., *Acalla* Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Pyrus Malus, Quercus, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2 245. 1910.

corylifoliella Haw., *Lithocolletis* Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, Malus, Sorbus.
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2 417. 1910.

crataegana Hub., *Cacoecia* Fam. *Tortricidae*
Synonym — *Penthina robrana* Schiff.
Hosts — Crataegus, Quercus, Betula, Populus, Malus, Cotoneaster, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872
Spuler, A Schmetterlinge Europas, 2 247. 1910.

crataegella Clem., *Lithocolletis* Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, *Prunus serotina*.
Injury — Larva mines in leaf.
Distribution — North America.
References Braun, A. F. Amer. Ent Soc. Trans. 34 301. 1908
Wilson, H. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2 119. 1915.

crataegella Linn., *Scythropia* Fam. *Yponomeutidae*
Hosts — *Crataegus oxyacantha*, *Prunus spinosa*, Pyrus.
Injury — Larva spins a tent over the branch and eats the leaves within it.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 169. 1872.
Spuler, A. Schmetterlinge Europas, 2. 143. 1910.

crataegi Linn., *Aporia* (Fruit-tree pierid) Fam. *Pieridae*
Hosts — Crataegus, Pyrus, Malus, Prunus, Sorbus, Salix, Quercus, and other species.
Injury — Larva eats foliage, often stripping trees.
Distribution — Europe
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p 303. 1805.
Sasscer, E. R. Journ econ. ent. 11 126. 1918.

crataegi Zell., *Bucculatrix* Fam. *Lyonetiidae*
Host — Crataegus.
Injury — Larva mines in leaf and later feeds externally on leaf
Distribution — Europe.
Reference — Stainton, H. T. Natural history of the Tineina, 7 68. 1862.

crataegi Saund., *Catocala* Fam. *Noctuidae*
Host — Crataegus.
Injury — Larva feeds on foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 8 72. 1876.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 532. 1890.

crataegi Linn., *Trichiura* — Fam. *Lasiocampidae*
Hosts — Prunus, Crataegus, Corylus, Betula, Salix, Alnus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, I 114. 1908.

crataegifoliella Clem., *Nepticula* — Fam. *Nepticulidae*
Host — *Crataegus uniflora.*
Injury — Larva mines in leaf.
Distribution — Eastern United States.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 534. 1890.

crataegifoliella Clem., *Ornix* — Fam. *Gracilariidae*
Host — *Crataegus tomentosa.*
Injury — Larva mines in leaf.
Distribution — Eastern United States.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 534. 1890.
Dietz, W. G. Amer. Ent. Soc. Trans. 33 292. 1907.

cucullella Esp., *Lophopteryx* — Fam. *Notodontidae*
Synonym — *Notodonta cucullina* Hub.
Hosts — *Acer campestre*, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.

cucullatella Linn., *Nola* — Fam. *Nolidae*
Synonym — *Herrgia pallidulis* Hub.
Hosts — Prunus, Malus, Crataegus.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2 122. 1910.

cuculionella Chamb., *Rhynchaenus* Hawthorn fruit miner — Fam. *Curculionidae*
See page 1080

dactylina Grote, *Acronycta* — Fam. *Noctuidae*
See page 1073

defoliaria Linn., *Hibernia* Mottled umber moth — Fam. *Geometridae*
Hosts — Malus, Prunus, Betula, Corylus, Quercus, Crataegus, Pyrus, and other species.
Injury — Larvae defoliate trees.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 163. 1872.
Theobald, F. V. Insect pests of fruits, p. 58. 1909.

dispar Linn., *Lymantria* Gipsy moth — Fam. *Lymantriidae*
Hosts — Species a very general feeder on trees. Crataegus a favored food plant.
Injury — Larvae defoliate trees.
Distribution — Europe, Asia, New England States.
References — Spuler, A. Schmetterlinge Europas, I 131. 1908.
Mosher, F. H. U. S. Agr. Dept. Bul. 250. 1915.

disstria Hub., *Malacosoma* Forest tent caterpillar — Fam. *Lasiocampidae*
Hosts — Acer, Quercus, Crataegus, Malus, and other species.
Injury — Larvae defoliate branches, feeding in colonies.
Distribution — North America.

References — Insect life 3 478. 1890.
Insect life 4 75. 1891.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 119. 1914.

dubitata Linn., *Triphosa* Fam. *Geometridae*
Hosts — Crataegus, Prunus, Rhamnus.
Injury — Larva webs leaves together and feeds on them.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 166. 1872.
Spuler, A. Schmetterlinge Europas, 2 36. 1910.

ephemeraeformis Haw., *Thyridopteryx* (Common bagworm) Fam. *Psychidae*
Hosts — Species a very general feeder on trees and shrubs, including Crataegus.
Injury — Larva defoliates trees.
Distribution — North America east of Rocky Mountains.
Reference — Beutenmueller, William. Ent. Amer. 3 157. 1887.

ephippella Fabr., *Argyresthia* Fam. *Yponomeutidae*
Synonym — *Argyresthia prunella* Linn.
Hosts — Crataegus, Pyrus, Prunus, Sorbus, Corylus.
Injury — Larva eats leaf and blossom buds.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2 447. 1910.

euphorbiae Fabr., *Acronycta* Fam. *Noctuidae*
Hosts — Species a general feeder on trees, including Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 139. 1908.

fabriciana Linn., *Simaethis* Fam. *Glyphipterygidae*
Synonyms — *Tinea oxyacanthella* Linn., *Crambus oxyacanthae* Fabr.
Hosts — Urtica, Parietaria, Symphytum, Crataegus.
Injury — Larva feeds in leaf roll.
Distribution — Europe.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p. 805. 1805.
Spuler, A. Schmetterlinge Europas, 2 297. 1910.

fasciellus Hub., *Holcophora* Fam. *Gelechiidae*
Hosts — Prunus, Crataegus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2 354. 1910.

fletcherella Fern., *Coleophora* (Cigar case-bearer) Fam. *Elachistidae*
Hosts — Malus, Crataegus Pyrus, Cydonia.
Injury — Larva eats holes into leaf and makes a small blotch mine around each hole.
Distribution — North America.
References — Hammar, A. G. U. S. Ent. Bur. Bul. 80, 33. 1909.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 47. 1914.

fulminea Scop., *Catocala* Fam. *Noctuidae*
Synonym — *Catocala paranympha* Linn.
Hosts — Crataegus, Prunus, Pyrus, Quercus.
Injury — Larva eats foliage.

Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 317. 1908.

geminatella Pack., *Ornix* - Unspotted tentiform leaf miner of apple — Fam. *Gracilariidae*
Synonym — *Lithocolletis pruniviorella* Chamb.
Hosts - Crataegus, Pyrus, Prunus.
Injury — Larva mines in leaf.
Distribution - Eastern United States.
Reference - Haseman, L. Journ. agr. res. 6 289. 1916.

glaucatus Schiff., *Cilix* — Fam. *Drepanidae*
Hosts — Prunus, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 107. 1908.

gothica Linn., *Taeniocampa* — Fam. *Noctuidae*
Hosts - Crataegus, Tilia, Quercus, and other species.
Injury - Larva feeds on foliage.
Distribution - Europe, Asia.
References - Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 239. 1908.

gratiosella Stt., *Nepticula* — Fam. *Nepticulidae*
Host - *Crataegus oxyacantha*
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2 476. 1910.

gratana T., *Dichelia* — Fam. *Tortricidae*
Hosts — Crataegus, Quercus, Ulmus, Rubus, and other species.
Injury — Larva ties leaves in bunch and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2 246. 1910.

hellerella Dup., *Blastodacna* — Fam. *Gelechiidae*
Hosts — Crataegus, Malus, Pyrus.
Injury — Larva tunnels in fruit of Crataegus and in fruit spurs and buds of apple.
Distribution — Europe.
References — Theobald, F. V. Insect pests of fruits, p. 92. 1909.
Spuler, A. Schmetterlinge Europas, 2 387. 1910.

hemerobiella Scop., *Coleophora* — Fam. *Eriocraniidae*
Hosts — Crataegus, Pyrus, Prunus.
Injury — Larva eats star-shaped area from under side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2 400. 1910.

heparana Schiff., *Pandemis* — Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Sorbus, Malus, Alnus, Betula, Fagus, and other species.
Injury — Larva rolls leaf and feeds within the roll.
Distribution — Europe, Japan.
Reference — Spuler, A. Schmetterlinge Europas, 2 249. 1910.

holmiana Linn., *Aciilla* — Fam. *Tortricidae*
Hosts — Crataegus, Rosa, Prunus, Malus, Pyrus, Quercus.

Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2. 244. 1910.

ignobilella Stt., *Nepticula* Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, 2. 477. 1910.

incerta Hufn., *Taeniocampa* Fam. *Noctuidae*
Synonym — *Taeniocampa instabilis* Hub.
Hosts — Crataegus, Salix, Prunus, Quercus, Malus, and other species.
Injury — Larva eats leaves, and sometimes eats holes in apple fruit.
Distribution — Europe, Asia, South America.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 66. 1909.

indigenella Zell., *Mineola* (Leaf crumpler) Fam. *Pyralidae*
Synonyms — *Acrobasis nebulella* Riley, *Phycita nebulo* Walsh.
Hosts — Malus, Crataegus, *Hicoria pecan*, and other species
Injury — Larva feeds on leaves, living in a case composed of leaf particles and silk.
Distribution — North America
Reference — Riley, C. V. Fourth Missouri report, p. 42. 1872.

integerrima G. and R., *Datana* (Black-walnut caterpillar) Fam. *Notodontidae*
Hosts — Juglans, Hicoria, Malus, Crataegus, and other species.
Injury — Larvae defoliate branches, feeding in a colony.
Distribution — Eastern United States.
Reference — Packard, A. S. Nat. Acad. Sci. Memoir 1. 120. 1895.

insulatumella Chamb., *Ornix* Fam. *Gracilariidae*
Host — Crataegus.
Injury — Larva mines in upper surface of leaf.
Distribution — Eastern United States.
References — Chambers, V. T. Can. ent. 5. 48. 1873.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

io Fabr., *Automeris* Fam. *Saturniidae*
(See page 1073.)

janthinana Dup., *Grapholitha* Fam. *Tortricidae*
Synonym — *Tortrix incisana* Schiff.
Host — Crataegus.
Injury — Larva tunnels in fruit, then in twigs.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2. 294. 1910.

lacustrata Guen., *Mesoleuca* Fam. *Geometridae*
Hosts — Rubus, Betula, Crataegus, Salix.
Injury — Larva feeds on foliage.
Distribution — Northeastern North America, Europe.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 158. 1876.
Smith, J. B. Insects of New Jersey, p. 497. 1909.

lanestris Linn., *Eriogaster* Fam. *Lasiocampidae*
Hosts — Prunus, Crataegus, Betula, Tilia, Salix.

Injury — Larvae defoliate branches, feeding gregariously in a white tent of silk
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 117. 1908.

leucatella Clerck, *Recurvaria* Fam. *Gelechiidae*
Hosts — Crataegus, Pyrus, Prunus, Sorbus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872
Spuler, A. Schmetterlinge Europas, 2 356. 1910.

leucophaearia Schiff., *Hibernia* Fam. *Geometridae*
Hosts — Quercus, Crataegus, Prunus, and other species
Injury — Larva eats foliage
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2 98. 1910

leucostigma A. and S., *Hemerocampa* (White-marked tussock caterpillar Fam. *Lymantriidae*
(See page 1075.)

limbata Haw., *Nematocampa* Fam. *Geometridae*
Synonym — *Nematocampa plumetaria* Gurn
Hosts — Crataegus, Fragaria.
Injury — Larva eats foliage
Distribution — North America.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 471. 1876.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

parops Bdv. and Lec., *Strymon* Striped hair-streak Fam. *Lycaenidae*
Hosts — Malus, Crataegus, Prunus, Amelanchier, Salix, Quercus, and other species
Injury — Larva eats entire leaf and sometimes bores into fruit
Distribution — United States, Canada
References — Scudder, S. Butterflies of New England, 2 877. 1889
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 539. 1890

pulifera Linn. *Trichiosoma* Fam. *Nematidae*
Hosts — Sorbus, Crataegus, Malus
Injury — Larva eats leaves
Distribution — Europe
Reference — Spuler, A. Schmetterlinge Europas, 1 145. 1908

lunaria Schiff., *Selenia* Fam. *Geometridae*
Hosts — Malus, Prunus, Crataegus, and other species
Injury — Larva eats leaves
Distribution — Europe, Asia
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 165. 1872.

lutarea Haw., *Swammerdamia* Fam. *Yponomeutidae*
Synonym — *Swammerdamia oxyacanthella* Dup
Hosts — Crataegus, Sorbus
Injury — Larva eats parenchymous tissue of leaves, which it ties together
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210, 782. 1872
Spuler, A. Schmetterlinge Europas, 2 445. 1910

lutecoma G. and R., *Acronycta* Fam. *Noctuidae*
(See page 1073.)

lutcolata Linn., *Opisthograptis* Fam. *Geometridae*
Synonym — *Rumia crataegata* Linn.
Hosts — Crataegus, Prunus, Malus, Pyrus, Sorbus.
Injury — Larva eats foliage.
Distribution — Europe, Asia, northern Africa.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 165. 1872.

nigricius Guen., *Ennomos* Fam. *Geometridae*
(See page 1076.)

malifoliella Clem., *Tischeria* (Apple trumpet leaf-miner) Fam. *Gracilariidae*
Hosts — Malus, Crataegus.
Injury — Larva mines in upper side of leaf, widening the mine gradually as it grows.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Quaintance, A. L. U. S. Ent. Bur. Bul. 68 23. 1908.

malimalifoliella Braun, *Lithocolletis* (Spotted tentiform leaf miner of apple) Fam. *Gracilariidae*
Hosts — Malus, Cydonia, *Crataegus mollis*
Injury — Larva mines in under side of leaf.
Distribution — Eastern United States.
Reference — Braun, A. F. Amer. Ent. Soc. Trans. 34 300. 1908.

malivorella Riley, *Coleophora* (Pistol case-bearer) Fam. *Elachistidae*
(See page 1079.)

manteo Doub., *Heterocampa* Fam. *Notodontidae*
(See page 1074.)

marginaria Borekh., *Hibernia* Fam. *Geometridae*
Hosts — Crataegus, Betula, Quercus, Tilia, Populus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas. 2 99. 1910.
Pierce, W. D. Manual of dangerous insects. p. 132. 1917.

melinus Hub., *Strymon* (Common hair-streak) Fam. *Lycaenidae*
Hosts — Hops, beans, Crataegus, and other species
Injury — Larva eats leaves and sometimes bores into fruit.
Distribution — North America, Central America.
References — Scudder, S. Butterflies of New England, 2 850. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Crosby, C. R., and Leonard, M. D. Manual of vegetable garden insects, p. 84. 1918.

minstra Dru., *Datana* (Yellow-necked apple caterpillar) Fam. *Notodontidae*
(See page 1075.)

myopiforme Bkh., *Trochilium* Fam. *Sesiidae*
Hosts — *Malus malus*, *Pyrus communis*, *Prunus domestica*, Crataegus
Injury — Larva tunnels under bark of unhealthy trees.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas. 2 310. 1910.

myops A. and S., *Paonias* Fam. *Sphingidae*
Hosts — Prunus, Crataegus, Salix, Corylus, and other species.
Injury — Larva eats leaves.

Distribution — Eastern United States.
Reference — Packard, A. S. Fifth rept U. S. Ent. Comm., p. 525, 536. 1890

naevana Hub., *Rhopobota* Fam. *Tortricidae*
Hosts — Prunus, Crataegus, Malus, Rhamnus, Sorbus, Ilex, and other species
Injury — Larva eats leaves of new shoots and ties them together.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2 273. 1910

nanella Hub., *Recurvaria* (Lesser apple bud moth) Fam. *Gelechiidae*
Synonym — *Recurvaria crataegella* Busck.
Hosts — Crataegus, Malus, Pyrus, Prunus.
Injury — Larvae destroy opening buds, and mine in leaves in late summer.
Distribution — Europe, North America
References — Scott, E. W., and Paine, J. H. U. S. Agr. Dept. Bul. 113 1914.
Sanders, G. E., and Dustan, A. G. Canada Agr. Dept., Ent. Branch Bul. 10 33 1919

neustria Linn., *Malacosoma* Lackey moth Fam. *Lasiocampidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Populus, Betula, Quercus, and other species
Injury — Larva eats leaves, frequently defoliating fruit trees, and builds silken tent over colony
Distribution — Europe, Asia
References — Spuler, A. Schmetterlinge Europas, 1 115. 1908.
Theobald, F. V. Insect pests of fruits, p. 30 1909.

nitidella Fabr., *Argyresthia* Cherry fruit moth Fam. *Yponomeutidae*
Hosts — Prunus, Crataegus.
Injury — Larva destroys young shoots of hawthorn, and bores into cherry fruit
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211 1872
Theobald, F. V. Insect pests of fruits, p. 192 1909
Spuler, A. Schmetterlinge Europas, 2 147 1910.

nitidella Heyn., *Nepticula* Fam. *Nepticulidae*
Host — *Crataegus oxyacantha*.
Injury — Larva mines in leaf
Distribution — Southwestern Germany
Reference — Spuler, A. Schmetterlinge Europas, 2 174 1910

nubeculana Clerc., *Aspidia* Fam. *Tortricidae*
See page 1077

nubilana Hub., *Cnephasia* Fam. *Tortricidae*
Hosts — Crataegus, Pyrus, Prunus, Malus, Betula.
Injury — Larva feeds between leaves tied together with silk
Distribution — Europe
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872
Spuler, A. Schmetterlinge Europas, 2 253. 1910

occidentalis G. and R., *Acronycta* Fam. *Noctuidae*
See page 1074

ocellana Fabr., *Tmetocera* Bud moth Fam. *Tortricidae*
Hosts — Crataegus, Sorbus, Malus, Pyrus, Cydonia, Prunus, Rubus, and other species
Injury — Larva destroys buds in early spring, and later ties the leaves together on them
Distribution — Europe, North America.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 192. 1872.
Slingerland, M. V. Cornell Univ. Agr. Exp. Sta. Bul. 107. 1896.
Theobald, F. V. Insect pests of fruits, p. 82. 1909.

oleagina Fabr., *Valeria* Fam. *Noctuidae*
Hosts — Crataegus, Prunus.
Injury — Larva feeds on foliage at night.
Distribution — Southern Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 1 185. 1908.

occasella Clem., *Argyresthia* Fam. *Yponomeutidae*
(See page 1078.)

oxyacanthae Frey, *Lithocolletis* Fam. *Gracilariidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in under side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, 2 415. 1910.

oxyacanthae Linn., *Miselia* Fam. *Noctuidae*
Host — *Crataegus oxyacantha.*
Injury — Larva eats foliage at night.
Distribution — Europe, Asia Minor.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schadlichen Forstinsekten, p. 504. 1805.
Spuler, A. Schmetterlinge Europas, 1 204. 1908.

oxyacanthella Stt., *Nepticula* Fam. *Nepticulidae*
Hosts — *Crataegus oxyacantha, Malus malus*, Sorbus
Injury — Larva mines in leaf on upper side.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 199. 1872.
Spuler, A. Schmetterlinge Europas, 2 474. 1910.

padellus Linn., *Yponomeuta* (Hawthorn ermine moth) Fam. *Yponomeutidae*
Synonym — *Hyponomeuta padella* Linn.
Hosts — Crataegus, Prunus, Vitis.
Injury — Larvae mine in leaves while young, then skeletonize leaves while living colonially in tents.
Distribution — Europe, North America (recently imported).
References — Theobald, F. V. Insect pests of fruits, p. 86. 1909.
Parrott, P. J. Journ. econ. ent. 11 55. 1918.

pariana Clerck., *Simaethis* Fam. *Glyphipterygidae*
Hosts — Malus, Sorbus, Crataegus, Betula, Prunus.
Injury — Larva makes a slight web over the leaf, then skeletonizes it.
Distribution — Europe, Asia Minor, North America (recently imported).
References — Spuler, A. Schmetterlinge Europas, 2 297. 1910.
Felt, E. P. New York State Mus. Bul. 202, 33. 1917.

pedaria Fabr., *Phigalia* Fam. *Geometridae*
Hosts — Pyrus, Quercus, Betula, Prunus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 164. 1872.
Spuler, A. Schmetterlinge Europas, 2 100. 1910.

podalirius Linn., *Papilio* — Fam. *Papilionidæ*
Hosts — Crataegus, Sorbus, Prunus, Amygdalus.
Injury — Larva eats foliage.
Distribution — Southern and central Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 1: 2. 1908.

polygrammata Guen., *Catocala* — Fam. *Noctuidæ*
Host — Crataegus.
Injury — Larva feeds on foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 8: 72. 1876.
Edwards, H. U. S. Nat. Mus. Bul. 35: 97. 1889.

polyphemus Cram., *Telea* — Fam. *Saturniidæ*
Hosts — Quercus, Ulmus, Juglans, Hicoria, Tilia, Betula, Rosa, Crataegus, and others.
Injury — Larva feeds on foliage.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Dickerson, Mary C. Moths and butterflies, p. 169. 1901.

prometheus Peck, *Alsophila* — Fall canker-worm — Fam. *Geometridæ*
(See page 1076)

pumifolella Clem., *Bucculatrix* — Ribbed-cocoon-maker of apple — Fam. *Lyonetiidæ*
(See page 1079)

pomonella Linn., *Cydia* — Codling moth — Fam. *Tortricidæ*
Hosts — Malus, Pyrus, Cydonia, occasionally Crataegus, Rosa, Prunus, *Juglans regia*
Injury — Larva bores in fruit.
Distribution — Europe, Asia, North America, Africa, Australia.
References — Bruner, L. Nebraska State Hort. Soc. Rept. 1894: 216. 1894.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 10. 1914.

populi Linn., *Poecilocampa* — Fam. *Lasiocampidæ*
Hosts — Populus, Tilia, Quercus, Ulmus, Betula, Salix, Crataegus, Malus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 34. 1909.

porrinata Zell., *Nemoria* — Fam. *Geometridæ*
Hosts — Corylus, Crataegus, and other species.
Injury — Larva eats leaves.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 2: 4. 1910.

praefica Grote, *Prodenia* (Yellow-striped army worm) — Fam. *Noctuidæ*
Hosts — *Medicago sativa*, Vitis, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Pacific coast of the United States.
References — Essig, E. O. Injurious and beneficial insects of California, p. 1915 [illegible] insects.
Crosby, C. R., and Leonard, M. D. Manual of vegetable garden insects, p. 295. 1918.

prunetorum Stt., *Nepticula* . . Fam. *Nepticulidae*
Hosts — Prunus, Crataegus.
Injury — Larva mines in leaf.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2 476. 1910.

pruniana Hub., *Argyroploce* Fam. *Tortricidae*
Hosts — Prunus, Sorbus, Rosa, Salix, Crataegus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2 265. 1910.

prunivora Walsh, *Laspeyresia* (Lesser apple worm) . Fam. *Tortricidae*
Hosts — Crataegus, Malus, Prunus.
Injury — Larva bores in fruit.
Distribution — North America east of Rocky Mountains.
Reference — Quaintance, A. L. U. S. Ent. Bur. Bul. 68:49. 1908.

psi Linn., *Acronycta* (Dagger moth) Fam. *Noctuidae*
Hosts — Malus, Prunus, Crataegus, Salix, Rosa, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 41. 1909.

pudibunda Linn., *Dasychira* (Red-tail moth) Fam. *Lymantriidae*
Hosts — Species a general feeder on fruit and forest trees. Crataegus a favored food plant.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas, 1:129. 1908.
Sorauer, P. Handbuch der Pflanzenkrankheiten, 3:384. 1913.

purpuralis Linn., *Pyrausta* . . . . Fam. *Pyralidae*
Hosts — Mentha, Nepeta, Plantago, Crataegus.
Injury — Larva feeds on leaves spun together with silk.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:236. 1910.

pygmaeella Haw., *Nepticula* . Fam. *Nepticulidae*
Hosts — *Crataegus oxyacantha*, *Malus mains*.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 199. 1872.
Spuler, A. Schmetterlinge Europas, 2:473. 1910.

pyramidea Linn., *Amphipyra* . . . . Fam. *Noctuidae*
Hosts — Crataegus and many other trees.
Injury — Larva eats foliage.
Distribution — Europe, Asia, East Indies.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:238. 1908.

pyramidoides Guen., *Amphipyra* . . . Fam. *Noctuidae*
Hosts — Crataegus and many other trees.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 171, 536 1890.

pyri Harris, *Aegeria* (Pear borer — Fam. *Sesiidae*
Synonym — *Sesia pyri* Boisd.
Hosts — Pyrus, Malus, Crataegus, Amelanchier, Prunus.
Injury — Larva burrows in bark and sapwood.
Distribution — Eastern United States.
Reference — Brooks, F. E. U. S. Agr. Dept. Bul. 887. 1920.

pyrina Linn., *Zeuzera* (Leopard moth — Fam. *Cossidae*
Synonym — *Zeuzera aesculi* Linn.
Hosts — Pyrus, Malus, Prunus, Crataegus, Fraxinus, Populus, Betula, Ulmus, and other species.
Injury — Larva mines in solid healthy wood of branches.
Distribution — Europe, Asia, Japan, North America.
References — Lintner, A. J. Ninth report on injurious insects of New York, p. 120. 1893.
Theobald, F. V. Insect pests of fruits, p. 46. 1909.

quadrifasciana Fern., *Eulia* — Fam. *Tortricidae*
See page 1078.

quercifolia Linn., *Gastropacha* (Lappet moth — Fam. *Lasiocampidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Quercus, and other species.
Injury — Larvae defoliate branches, especially of nursery trees, in spring.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1: 122. 1908.
Collinge, W. E. Manual of injurious insects, p. 137. 1912.

querna Linn., *Lasiocampa* — Fam. *Lasiocampidae*
Hosts — Crataegus, Quercus, Betula, Salix, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1: 118. 1908.

quernaria A. and S., *Nascopora* — Fam. *Geometridae*
Hosts — Quercus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 111. 1876.
Edwards, H. U. S. Nat. Mus. Bul. 35: 106. 1889.

radiatella Harr., *Argyresthia* — Fam. *Yponomeutidae*
See page 1074.

regiella H. S., *Nepticula* — Fam. *Nepticulidae*
Host — *Crataegus oxyacantha*.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, 2: 475. 1910.

rhediella Clerck, *Pamene* — Fam. *Tortricidae*
Hosts — Crataegus, Malus, Prunus, Cornus.
Injury — Larva feeds in fruit of Crataegus and also eats leaves.
Distribution — Europe, Asia Minor.
References — Theobald, F. V. Insect pests of fruits, p. 80. 1909.
Spuler, A. Schmetterlinge Europas, 2: 296. 1910.

rheana Hub., *Pandemis* . . Fam. *Tortricidae*
Hosts — Crataegus, Rosa, Prunus, Malus, Pyrus, Quercus, Sorbus, and other species.
Injury — Larva ties several leaves together and feeds within.
Distribution — Europe, Asia, Japan, East Indies.
Reference — Spuler, A. Schmetterlinge Europas, 2 249. 1910.

rosaceana Harris, *Cacoecia* (Oblique-banded leaf roller) Fam. *Tortricidae*
Hosts — Crataegus, Malus.
Injury — Larvae tie leaves together and feed on them.
Distribution — North America.
References — Essig, E. O. Injurious and beneficial insects of California, p. 441 1915.
Sanders, G. E., and Dustan, A. G. Canada Agr. Dept., Ent. Branch. Bul. 16 30. 1919.

rosana Linn., *Cacoecia* Fam. *Tortricidae*
Synonym — *Tortrix laevigana* Schiff.
Hosts — Malus, Crataegus, Pyrus, Prunus, and other species.
Injury — Larvae tie leaves together and feed on them.
Distribution — Europe, Asia Minor, North America.
References — Theobald, F. V. Insect pests of fruits, p. 80. 1909.
Sorauer, P. Handbuch der Pflanzenkrankheiten, 3 299. 1913.

scintillans Braun, *Nepticula* Fam. *Nepticulidae*
Host — *Crataegus mollis.*
Injury — Larva mines in leaf.
Distribution — Ohio.
Reference — Braun, A. F. Amer. Ent. Soc. Trans. 43 167. 1917.

scitella Zell., *Cemiostoma* (Pear leaf blister moth Fam. *Lyonetiidae*
Hosts — Crataegus, Pyrus, Prunus, Sorbus.
Injury — Larva mines in leaf.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 197. 1872.
Theobald, F. V. Insect pests of fruits p. 330. 1909.
Spuler, A. Schmetterlinge Europas, 2 223. 1910.

scitula Harris, *Sesia.* Fam. *Sesiidae*
(See page 1076.)

sclerana Guen., *Ancylis* Fam. *Tortricidae*
Hosts — Pyrus, Malus, Crataegus.
Injury — Larva ties leaves together and feeds within.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2 270. 1910.

signatana Dgl., *Steganoptycha* Fam. *Tortricidae*
Synonym — *Grapholitha kroesmanniana* Hein.
Hosts — Prunus, Crataegus.
Injury — Larva eats young terminal leaves after tying them with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2 276. 1910.

similis Fuessl., *Porthesia* (Gold-tail moth) . . . . . Fam. *Lymantriidae*
Synonym — *Liparis auriflua* Hub.
Hosts — Crataegus and most other fruit and non-coniferous forest trees.
Injury — Larva eats foliage.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1: 133. 1908.

sphinx Hufn., *Brachionycha* . . . Fam. *Noctuidæ*
Synonym — *Asteroscopus cassinia* S. V.
Hosts — Quercus, Populus, Malus, Prunus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia Minor.
References Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1: 203. 1908.

spiniana Dup., *Pamene* Fam. *Tortricidæ*
Hosts — Crataegus, Prunus, Alnus.
Injury — Larva feeds in blossom, destroying it.
Distribution — Europe, northern Africa.
Reference — Spuler, A. Schmetterlinge Europas, 2: 295. 1910.

splendoriferella Clem., *Coptodisca* Resplendent shield-bearer Fam. *Elachistidæ*
Hosts — Malus, Crataegus, *Prunus serotina*, Pyrus, Cydonia
Injury — Larva mines in leaf and cuts out a small piece of the leaf for its case.
Distribution — Northeastern United States
References Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 526. 1890.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 75. 1914.

spurcella H.-S., *Gelechia* Fam. *Gelechiidæ*
Hosts — *Prunus spinosa*, *Crataegus oxyacantha*
Injury — Larva rolls leaves.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2: 361. 1910.

steinkellneriana Schiff., *Epagraphia* Fam. *Gelechiidæ*
Hosts — Crataegus, Sorbus, *Prunus spinosa*, Fraxinus
Injury — Larva ties leaves together and eats them.
Distribution — Europe.
References Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2: 332. 1910.

stimulea Clem., *Sibine*, Saddle-back caterpillar Fam. *Limacodidæ*
Hosts — Species a general feeder on fruit and forest trees, including Crataegus.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References Beutenmuller, William. Ent. Amer. 4: 75. 1888.
Dyar, H. G., and Morton, E. L. New York Ent. Soc. Journ. 4: 1. 1896.

strigata Müll., *Hemithea* Fam. *Geometridæ*
Synonym — *Nemoria nestaria* Hub.
Hosts — Quercus, Crataegus, Corylus, Syringa, Malus, Prunus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References Kaltenbach, J. H. Pflanzenfeinde, p. 163. 1872.
Spuler, A. Schmetterlinge Europas, 2: 5. 1910.

strigosa Fabr., *Acronycta* Fam. *Noctuidæ*
Hosts — Prunus, Crataegus, Rhamnus.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
Reference — Spuler, A. Schmetterlinge Europas, 1: 137. 1908.

subsignarius Hub., *Eunomos* Fam. *Geometridae*
(See page 1076.)

suffusana Z., *Notocelia* Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Pyrus, Malus.
Injury — Larva ties together leaf cluster and feeds within, also eats leaf buds.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2 279. 1910.

superans Guen., *Acronycta* Fam. *Noctuidae*
(See page 1074.)

tesselaris A. and S., *Halisidota* Fam. *Arctiidae*
(See page 1073.)

textor Harris, *Hyphantria* (Fall webworm) Fam. *Arctiidae*
(See page 1073.)

thysbe Fabr., *Hemaris* Fam. *Sphingidae*
Hosts — Viburnum, Symphoricarpus, Crataegus.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Fernald, C. H. Sphingidae of New England, p. 16. 1886.
Beutenmueller, William. Hawk moths of the vicinity of New York City, p. 9. 1903.

tiliaria Harris, *Erranis* (Lime-tree spanworm) Fam. *Geometridae*
(See page 1076.)

tineana Hub., *Ancylis* Fam. *Tortricidae*
Hosts — Populus, Crataegus, Prunus, Malus.
Injury — Larva eats foliage after tying it with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2 270. 1910.

turbata Cr., *Pseudophia* Fam. *Noctuidae*
Synonym — *Ophiusa turrhaea* Cr.
Hosts — Rhus, Pistacia, Crataegus.
Injury — Larva eats foliage.
Distribution — Southern Europe, Asia, Africa, Australia, and islands of southern Pacific.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 512. 1908.

tilia Cram., *Phigalia* Fam. *Geometridae*
(See page 1076.)

trapezina Linn., *Calymnia* Fam. *Noctuidae*
Hosts — Quercus, Salix, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 244. 1908.

tridens Schiff., *Acronycta* Fam. *Noctuidae*
Hosts — Crataegus, Prunus, Malus, Rosa, Salix, Rhamnus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1 137. 1908.

turnus Linn., *Papilio* (Tiger swallowtail) — Fam. *Papilionidæ*
Hosts — Crataegus, Malus, Cydonia, Prunus, Betula, Tilia, Quercus, Salix, and other species.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 6: 2. 1874
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890

unicornis A. and S., *Schizura* — Fam. *Notodontidæ*
Hosts — Malus, Prunus, Crataegus, Ulmus, Populus, Corylus, Quercus, and other species.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Packard, A. S. Nat. Acad. Sci. Memoir 1: 203. 1895.

ursipana Hub., *Olethreutes* — Fam. *Tortricidæ*
Hosts — Malus, Pyrus, Crataegus, Prunus, and other species.
Injury — Larva ties leaf clusters together and eats leaves and buds.
Distribution — Europe, Asia.
References — Newstead, R. Gard. chron. 1901: 342. 1901
Theobald, F. V. Insect pests of fruits, p. 82. 1909

vernata Peck, *Paleacrita* (Spring cankerworm) — Fam. *Geometridæ*
Hosts — Ulmus, Malus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Wilhous, W. H. Univ. Kans., Ent. Dept. Bul. 11: 283. 1917

vetusta Boisd., *Homoeosoma* (Western sunflower moth) — Fam. *Pyralidæ*
Hosts — Malus, Prunus, Crataegus, Juglans, Quercus, and other species.
Injury — Larva eats leaves and sometimes young fruit.
Distribution — Pacific coast of the United States.
References — Branigan, F. J. State Comm. Hort. California. Mo. bul. 3: 245. 1914
Essig, E. O. Injurious and beneficial insects of California, p. 408. 1915

vorax Walch., *Odontopera* — Fam. *Noctuidæ*
Hosts — Prunus, Crataegus, Pyrus.
Injury — Larva eats foliage at night.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas. 1: 204. 1908

vulgata Linn., *Nemeria* — Fam. *Geometridæ*
Hosts — Calluna, Crataegus, Rubus, Quercus, Betula, Corylus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 235. 1872
Spuler, A. Schmetterlinge Europas. 2: 1. 1910

vulpata Haw., *Tephroclystia* — Fam. *Geometridæ*
Hosts — Crataegus, Polygonum, Rubus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 300. 1872
Spuler, A. Schmetterlinge Europas. 2: 75. 1910.

wahlella Hub., *Gelechia* — Fam. *Gelechiidæ*
Hosts — Crataegus, Prunus.

Injury – Larva ties together a cluster of leaves and feeds within.
Distribution – Europe.
References – Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2 358. 1910.

DIPTERA

bsobrina Felt, *Rhizomyia* Fam. *Cecidomyiidae*
Hosts – Crataegus, Populus, *Prunus virginiana*.
Injury – Larva found in leaf gall.
Distribution – North America
Reference Felt, E. P. New York State Mus. Bul. 200 138. 1918.

nthobia F. Loew, *Contarina* Fam. *Cecidomyiidae*
Host – *Crataegus oxyacantha*.
Injury – Solitary larva feeds in blossom bud, causing it to remain closed and swollen.
Distribution – Europe
References – Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911.
Bagnall, R. S., and Harrison, J. W. H. Ent. Soc. London. Trans. 1917. 391. 1917.

adequar Walsh, *Cecidomyia* (Tufted thorn gall) Fam. *Cecidomyiidae*
Host – Crataegus.
Injury – Larvae deform leaves with filamentous subglobular vein galls, 1 cm. long, generally found on the midveins.
Distribution – North America.
References – Walsh, B. D. Can. ent. 1 79. 1869.
Felt, E. P. New York State Mus. Bul. 200 138. 1918.

crassifolia Felt, *Mycodiplosis*. Fam. *Cecidomyiidae*
Hosts – *Prunus virginiana*, Crataegus.
Injury – Larvae live in galls on hawthorn fruit caused by *Gymnosporangium clavipes*, and feed on the rust spores.
Distribution – North America
References – Felt, E. P. New York State Mus. Bul. 200 152. 1918.
Wellhouse, W. H. Ent. news 30 144. 1919.

incumdata Winn., *Perrisia* Fam. *Cecidomyiidae*
Host – *Crataegus oxyacantha*.
Injury – Larva lives in leaf gall.
Distribution – Germany
References – Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
Kieffer, J. J. Genera insectorum, fasc. 152, p. 75. 1913.

crataegi Winn., *Perrisia* Fam. *Cecidomyiidae*
Host – *Crataegus oxyacantha*.
Injury – Colonies of larvae cause rosettes of deformed sessile leaves, which make trees and hedges unsightly.
Distribution – Europe.
References – Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
Connold, E. T. British vegetable galls, p. 190. 1902.

crataegifolia Felt, *Hormomyia* (Thorn cockscomb gall) Fam. *Cecidomyiidae*
Host – Crataegus.
Injury – Larva deforms leaf with a green or red gall 1 cm. long, shaped like a cockscomb.
Distribution – United States.
References – Felt, E. P. Journ. econ. ent. 1 20. 1908.
Felt, E. P. New York State Mus. Bul. 200 136. 1918.
(Figs. 116 and 117, page 1082.)

crataegifolia Felt, *Lestodiplosis* (Hawthorn fringed-cup gall) Fam. *Cecidomyiid*
Host — Crataegus.
Injury — Larva causes a gall on leaf or twig.
Distribution — United States.
References — Felt, E. P. New York State Mus. Bul. 124: 108. 1908
Felt, E. P. New York State Mus. Bul. 200: 138. 1918
(Figs. 114 and 115, page 1081.)

excavata Felt, *Lasioptera* (Purple leaf blotch) Fam. *Cecidomyiidæ*
Host — Crataegus.
Injury — Larvæ deform leaves with green or reddish, blister-like mines, about 8 mm. in diameter.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200: 138. 1918.

hirta Felt, *Rhopalomyia* Fam. *Cecidomyiidæ*
Host — Crataegus.
Injury — Species probably inquiline in blister mine made by *Lasioptera excavata*.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200: 138. 1918.

hudsonica Felt, *Winnertzia* Fam. *Cecidomyiidæ*
Host — Crataegus.
Injury — Larva deforms leaf with stout, cup-shaped, fimbriate, unicellular gall.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200: 138. 1918.

pomonella Walsh, *Rhagoletis* Apple maggot Fam. *Trypetidæ*
Hosts — Crataegus, Malus, Vaccinium, Symphoricarpos.
Injury — Larva tunnels in fruit.
Distribution — Eastern North America.
References — Walsh, B. D. First annual report on noxious insects of Illinois, p. 30. 1868.
O'Kane, W. C. New Hampshire Agr. Exp. Sta. Bul. 171. 1914.
Severin, H. H. P. State Comm. Hort. California. Mo. bul. 7: 430. 1918.

venae Felt, *Lobopteromyia* Thorn vein gall Fam. *Cecidomyiidæ*
Host — Crataegus.
Injury — Larva causes oval, smooth, fleshy gall, 5 to 8 mm. long, on leaf vein.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200: 138. 1918.
Figs. 118 and 119, page 1083.

venatilis Felt, *Dirrodiplosis* Fam. *Cecidomyiidæ*
Host — Crataegus.
Injury — Larva found in same gall with *Lobopteromyia venae*.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200: 138. 1918.

Cecidomyia sp. a. 2727 Felt Fam. *Cecidomyiidæ*
Host — Crataegus.
Injury — Larvæ cause subglobose, greenish, sometimes confluent, frequently [illegible] polythalamous vein galls, the under side reddish, diameter 3 mm.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200: 138. 1918.

Cecidomyia sp. a. 1540 Felt. (Thorn spindle gall) Fam. *Cecidomyiidæ*
Host — Crataegus.

Injury — Larva causes a spindle-shaped thickened gall on leaf vein, green or reddish, length 1 cm., diameter 2 mm.
Distribution — Eastern United States.
Reference — Felt, E. P. New York State Mus. Bul. 200. 138. 1918.
(Figs. 120 and 121, page 1084.)

HYMENOPTERA

betuleti Klg., *Trichiosoma* Fam. *Tenthredinidae*
Synonyms — *Cimbex crataegi* Wd., *Trichiosoma tibialis* Steph.
Host — Crataegus.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1: 27. 1879.

cerasi Linn., *Caliroa* (Pear and cherry slug) . . Fam. *Tenthredinidae*
Hosts — Prunus, Crataegus, Pyrus, and other species.
Injury — Larvae skeletonize leaves.
Distribution — Europe, North America, Australia.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 214. 1914.
MacGillivray, A. D. Hymenoptera of Connecticut, p. 79. 1916.

collaris MacG., *Profenusa* (Cherry and hawthorn sawfly leaf miner) Fam. *Tenthredinidae*
Hosts — Crataegus, *Prunus cerasus*.
Injury — Larva mines in leaf, causing brown blister which may cover from a quarter to the whole of the upper surface of the leaf.
Distribution — Massachusetts, New York.
Reference — Parrott, P. J., and Fulton, B. B. New York (Geneva) Agr. Exp. Sta. Bul. 411. 1915.

dimidiatum Boh., *Syntomaspis* (Apple seed chalcid) Fam. *Chalcididae*
Hosts — Malus, Pyrus, Sorbus, Crataegus.
Injury — Oviposition punctures cause dimples in fruit, and larvae destroy seeds.
Distribution — Europe, North America.
References — Schlechtendall, D. von. Ztschr. Naturwiss. Halle 61: 415. 1888.
Cushman, R. A. Journ. agr. res. 7: 487. 1916.
Woodruffe-Peacock, E. A. Naturalist (London), no. 753, p. 329. 1919.

flaviventris Retz., *Lyda* Fam. *Tenthredinidae*
Synonym — *Lyda clypeata* Klg.
Hosts — Crataegus, Pyrus.
Injury — Larvae defoliate branches, feeding in colonies.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 206. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1: 516. 1879.

humeralis Fourc., *Cimbex* . . . Fam. *Tenthredinidae*
Synonym — *Cimbex axillaris* Pz.
Hosts — Crataegus, *Prunus padus*.
Injury — Larva feeds on foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1: 24. 1879.

padi Linn., *Priophorus* Fam. *Tenthredinidæ*

Hosts. — Crataegus, Pyrus, Prunus, Malus, Sorbus, and other species.
Injury. — Larva skeletonizes leaves.
Distribution. — Europe.
References. — André, Ed. Species des Hyménoptères d'Europe, I: 84. 1879.
Collinge, W. E. Manual of injurious insects, p. 219. 1912.

punctum-album Linn., *Macrophya* Fam. *Tenthredinidæ*

Hosts. — Fraxinus, Ligustrum, Crataegus.
Injury. — Larva feeds on foliage.
Distribution. — Europe.
Reference. — André, Ed. Species des Hyménoptères d'Europe, I: 359. 1879.

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